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North America (Testudines: Emydidae)**

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Relationships of Chrysemyd Turtles of North America (Testudines: Emydidae)

Joseph P. Ward

Some of the most distinctive inhabitants of North American freshwater communities are the "cooter" and "slider" turtles of the chrysemyd complex. Their conspicuousness is due to their large size and basking habits. In fact, these turtles are so visible in their environment that they are among the first American reptiles described by European naturalists. Although conspicuous, their extreme variability in external morphology created confusion among early taxonomists, who often treated each individual variant as a separate species. Description and redescription of individuals, occasionally from the same population, created a taxonomic morass. Original descriptions of many species were so vague that succeeding investigators were unable to distinguish between populations described and ones undescribed. Heightening the confusion was the lack of usable locality data or frequent lack of assigned museum numbering. The British Museum numbering system, for example, was not initiated until the late 1800's after many of the species had been described from specimens in that collection. To further complicate the situation, type specimens have been misplaced or lost.

As a result, the identification and relationships of the chrysemyd turtles continue to be a problem. Current taxonomic practice includes all slider and cooter species in a single genus, *Chrysemys* (hence the term chrysemyds, referring to all species included in the genus *Chrysemys*, *sensu* McDowell, 1964). This single genus concept has a number of problems. The differences between chrysemyd species are often greater than those between *Chrysemys* and other genera; for example, *C. picta* has up to 20 external morphological features that are rarely, if at all, found in other species of the genus (Galbreath, 1948; Carr 1952; Adler, 1968; Ward, 1980). Superficial skull resemblances (Boulenger, 1889; McDowell, 1964) within chrysemyds (namely *C. scripta*) prompted authorities to combine *Chrysemys* with *Pseudemys* and *Trachemys*. Data from electrophoresis (Vogt and McCoy, 1980), skull and shell morphology (Monks, 1878; Baur, 1893; Brimley, 1907; Galbreath, 1948; Carr and Crenshaw, 1957; Adler, 1968; Zangerl, 1969; Ward, 1980), parasites (Ernst and Ernst, 1980), physiology (Ward, 1970), ecology and behavior (Marchand, 1944; Cagle, 1950; Jackson and Davis, 1972; Petranka and Phillippi, 1978; Ward, 1980), however, indicate that the three genera are distinct. McDowell (1964) assumed that turtle skulls showed little intrageneric variation and found no differences in chrysemyd skulls in small samples. Even so, he recognized *C. picta* as an exception in several characters by which he defined the genus *Chrysemys*.

Other authors (Rose and Weaver, 1966; Weaver and Rose 1967; Weaver and Robertson, 1967) have tentatively supported McDowell's arrangement. Recently, the separation of *Chrysemys* and *Pseudemys* has been advocated by Adler (1968), Zangerl (1969), Moll and Legler (1971), Mount (1975), Holman (1977), Vogt and McCoy (1980), and Ward (1980).

The objective of this study is to examine a set of morphological features to test the validity of the assumed close relationships in chrysemyd turtles.

MATERIALS AND METHODS

This analysis examined three major character sets: cranial morphology, carapacial morphology, and cranial myology. The emphasis has been on an objective evaluation of skull structures by means of a quantitative analysis of osteological components, particularly those associated with the feeding mechanisms. Measurements were made with vernier calipers and are accurate to 0.1 mm. The terminology for cranial elements follows Gaffney (1972), as modified by Ward (1980).

A total of 38 straightline measurements were made on each skull. Although skulls of juveniles were examined, only those of adults were used in analysis of characters. A preliminary analysis showed that 31 of these parameters are useful in differentiating chrysemyd turtles. They are (Fig. 1):

Mandible:

- hc perpendicular height of the mandibular ramus measured to the highest point of the coronoid process from the ventral edge of the dentary.
- lmsa the length of the mandibular ramus measured from the anterior edge of the mandibular symphysis to the posterior edge of the articular bone.
- lmsj the length of the mandibular ramus from the anterior edge of the mandibular symphysis to the posterior edge of the triturating surface; hence the length of the alveolar shelf of the lower jaw along the longitudinal axis.
- th the thickness of the mandibular ramus measured just posterior to the coronoid process, across the Meckelian fossa.
- wma the width across the mandible (both rami), external edge to external edge, measured at the articular bones.
- wmj the width of the mandible, across both rami, between the lateral edges of the most posterior point of the alveolar shelf, just anterior to the coronoid process.
- ws the length of the mandibular symphysis measured on the ventral aspects of the dentary, along the symphysis, from the anterior-most aspect of the hook to the posterior most aspect of the dentary at the symphysis.
- wtm the width of the alveolar shelf of the mandible, measured at the most posterior point prior to the posterior narrowing of the shelf.
- wts the width of the lower alveolar shelf measured just posterolateral to the mandibular symphysis; this includes the length of the symphyseal ridge, but not the width of the symphysis (ws).

Cranium:

- ao the posterior length of the otic capsule, measured from the posteriodorsal edge of the squamosal, ventrad to the ventral edge of the quadrate articular condyle.
- bc basiocranial length from the occipital condyle to the most anterior edge of the premaxilla.

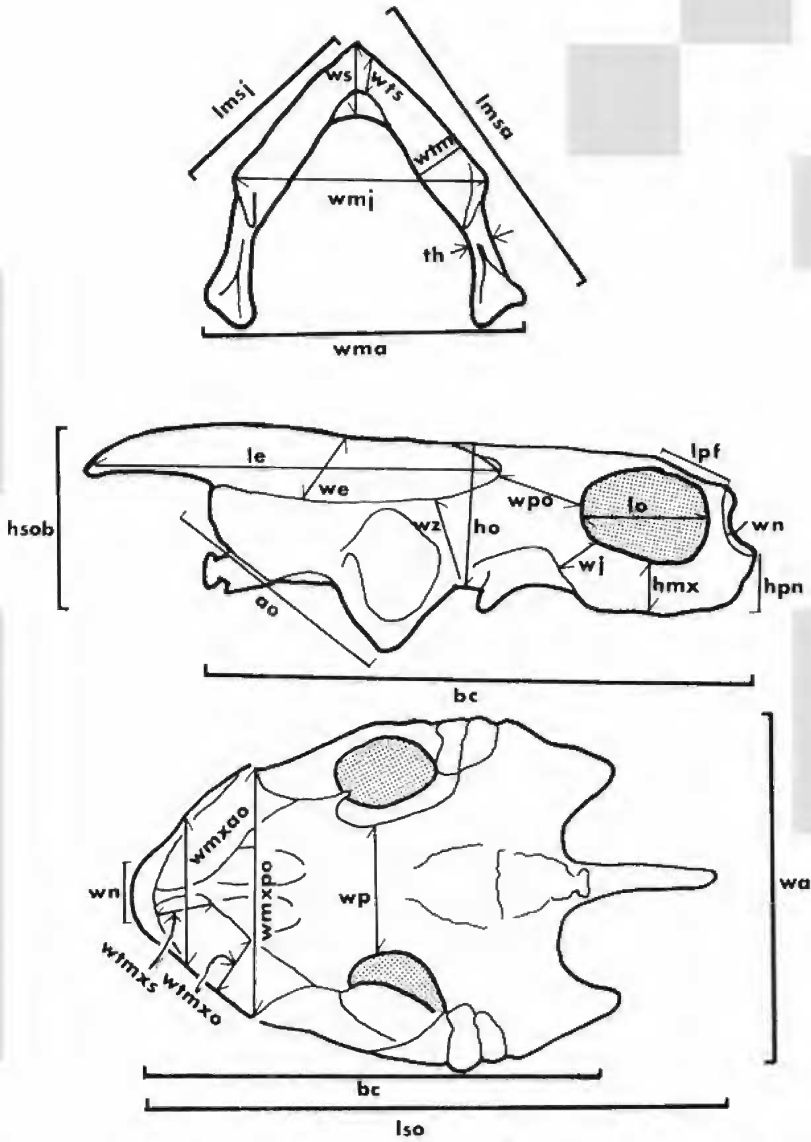


FIG. 1.—Cranial measurements for chrysemyd turtles. The abbreviations and a description of each measurement is given in the text. Top, dorsal aspect of mandible; middle, lateral aspect of skull; bottom, ventral aspect of skull.

- io interorbital width between the dorsal rims of the orbits measured at the frontal-prefrontal suture.
- hmx the external height of the maxilla at the mid-orbit from the ventral edge of the tomial ridge to the ventral rim of the orbit.
- ho the height of the cranium from the pterygoid to the parietal at the level of the base of the external pterygoid process.
- hpn the height of the premaxilla from the ventral tomial ridge to the ventral edge of the nasal fenestra.

hsob	height of the posterior skull from the ventral basioccipital to the ventral edge of the supraoccipital crest just dorsal to the foramen magnum.
le	the length of the posterior emargination of the skull (temporal fossa) from the posterior tip of the supraoccipital crest to the posterior edge of the postorbital arch.
lo	the horizontal diameter of the orbit at its midpoint.
lpf	the length of the interprefrontal suture plus half the length of the prefrontal process of the frontal.
lso	the total length of the skull from the posterior tip of the supraoccipital crest to the anterior edge of the prefrontal bone.
wa	the width of the skull across the lateral edges of the articular condyle (includes wma).
we	the width of the temporal fossa at its widest point.
wj	the width of the jugal process of the maxilla at the posterior edge of the orbit just ventral to the jugomaxillary suture.
wmxao	the width across the upper jaw, from tomial ridge to tomial ridge at the level of the anterior rim of the orbit.
wmxpo	width across the upper jaw or maxilla, from tomial ridge to tomial ridge, at the level of the posterior rim of the orbit, approximately the posterior edge of the alveolar shelf at its widest point.
wn	width of the nasal fenestra at the midpoint.
wp	width of both pterygoids measured at the closest proximity of the lateral edges posterior to the external pterygoid process (on the ventral surface).
wpo	width of the postorbital arch measured at its midpoint (narrowest point) from the posterior orbit rim to the anterior edge of the dorsal temporal fossa.
wz	width of the zygomatic arch measured at the anterior-most point of the posterior edge of the quadratojugal (quadratojugal suture), roughly on the level of the posterior edge of the coronoid bone of the lower jaw when adpressed.
wtmxo	the width of the upper alveolar shelf at the level of the posterior edge of the orbit; measured at the widest point of the shelf.
wtmxs	width of the upper alveolar shelf (tritulating surface) measured at the anterior edge of the shelf (approximately at the maxilla-premaxilla suture).

In addition, the total number of cusps on the medial ridge of the mandible was noted, as were the presence of tomiodonts and premaxillary notching.

Features of the carapace and cranial muscles were largely qualitatively examined. Carapacial characteristics are:

Mensural features:

cl	carapace length: straightline measurement along midline.
ch	carapace height at pectoral-abdominal scute seam.
cw	carapace width at the widest point.
pll	plastron length along midline.
nl	length of cervical scute.

Qualitative features:

cervical notch:	notch at midpoint of anterior edge of cervical scute.
cervical extension:	anterior extension of the leading edge of the cervical scute relative to that of the first marginal scute on either side.
free ribs: lengths:	relative lengths, to each other, of the free rib segments two, three and four;
free ribs: widths:	widths of the free rib segments to their own lengths.

keel: presence of a raised keel on the first or second vertebral scute.

marginal notch: notch in the outer edge of the posterior marginal scutes, midway between the seams.

rugosity: presence of longitudinally oriented grooves and ridges on pleural scute II, extending past both adjacent interpleural seams.

Muscle features noted include the presence or absence of certain muscles, differences in attachment of muscles, and the relative sizes of each muscle (or group of muscles). Muscle terminology follows Ward (1980) and is reviewed below.

The cranial musculature of chrysemyds can be viewed as seven groups, which are involved in three principal jaw movements: adduction, protraction, and retraction. Adductor muscles close the jaw, protractors move the jaw forward, and retractors depress or open the jaw. The seven groups (Figs. 2, 3) are: 1) adductor mandibularis externus, internus, and medialis, 2) adductor mandibularis anterior, 3) adductor mandibularis posterior, 4) pterygoideus, 5) depressor mandibularis, 6) branchiomandibularis, and 7) zygomaticomandibularis. The general attachment pattern of these muscles in chrysemyds follows:

Adductor mandibularis externus (composed of two long heads and a short head)

pars profundus—originates from the dorsal and medial ridges of the supraoccipital crest and from portions of the external tendon to insert directly and by the external tendon into the anterior external fossa of the mandible.

pars superficialis—arises on the lateral edge of the temporal fossa along the dorsomedial aspects of the squamosal and quadrate bones and inserts directly in the anterior external fossa and onto portions of the external tendon.

pars medius—arises along the trochlear ridge on the quadrate and inserts by a short tendon to the external tendon, to the anterior external fossa, and on the coronoid process; the insertion in the external fossa is slightly ventrolaterad of that of the external tendon.

Adductor mandibularis internus (composed of two muscles joined by a broad tendon, the internal tendon)

pseudotemporalis—arises on the descending process of the parietal, internal to the adductor mandibularis, and inserts onto the internal tendon.

intramandibularis—originates from the internal tendon to insert on the lateral aspects of the coronoid process and dentary.

Adductor mandibularis medialis—arises on the upper parietal, ventral aspects of the lateral process of the frontal, and from the posterior maxilla to insert on the posterodorsal dentary and lower external fossa.

Adductor mandibularis anterior—arises in the upper, anterior temporal fossa on the ascending process of the parietal and inserts dorsomedially on the external fossa; courses just anterior to the pars profundus above the temporal ridge, then turns internally to the pars profundus in the lower temporal fossa.

Adductor mandibularis posterior—arises along the trochlear ridge of the quadrate and prootic bones to insert vertically in the medial external fossa and edge of the Meckelian fossa just posterior to the coronoid.

Pterygoideus (two headed muscle)

pars dorsalis—arises from the internal pterygoid process to insert by a short tendon to the medial articular bone.

pars ventralis—arises on the upper and lower regions of the dorsal aspects of the external pterygoid process to insert on the ventromedial edges of the coronoid process and the anteromedial articular and prearticular.

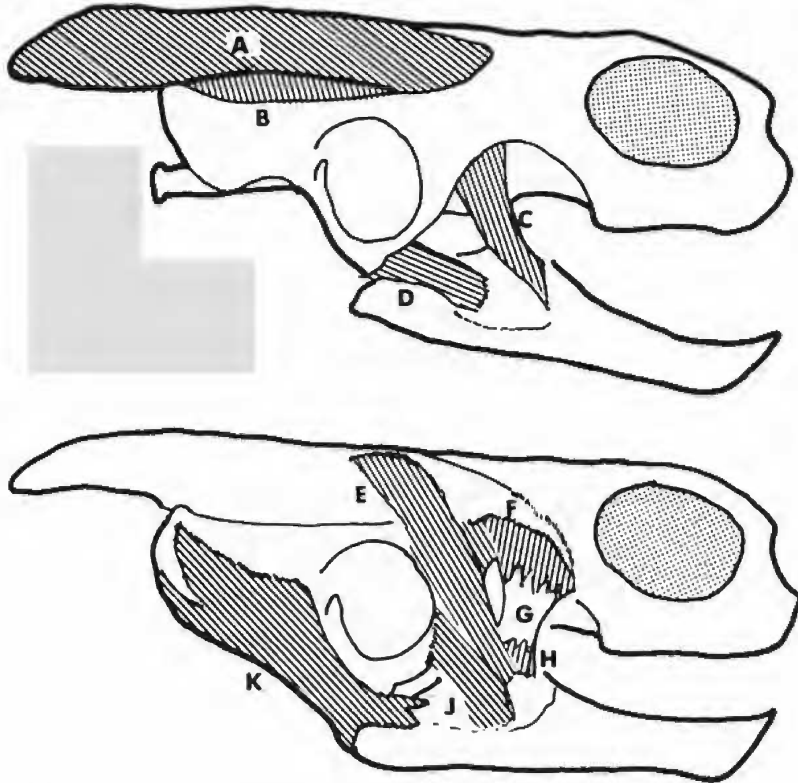


FIG. 2.—Diagrammatic representation of the major cranial muscles in a generalized chrysemyd. **Upper** (lateral view of skull with all muscle in place): A-D, adductor mandibularis externus; A, pars profundus; B, pars superficialis; C, external tendon; D, pars medius. **Lower** (lateral view, zygomatic arch and adductor mandibularis externus removed): E, adductor mandibularis anterior; F, pseudotemporalis; G, internal tendon; H, intramandibularis; J, adductor mandibularis posterior; K, depressor mandibularis.

Depressor mandibularis—arises from the dorsal and posterior aspects of the squamosal bone and the quadrate posteriorly to insert on the ventral, medial edge of the angular and articular.

Branchiomandibularis—arises on the first branchial segment and inserts on the angular and surangular along the ventro-medial side of the mandibular ramus just anterior to the insertion of the adductor groups.

Zygomatocomandibularis—thin muscle overlying the medialis; arises along the internal surface of the zygomatic arch (quadratojugal, jugal and postorbital bones) and inserts on the ventral edge of the external fossa.

The pectoral girdle was also examined to determine the usefulness of bone shapes and angles formed by the confluence of certain elements, particularly the angle between the acromium and the scapula and between the acromium and coracoid. The pattern of head stripes, the distribution of inframarginal spots, and the plastral patterns appear to indicate relationships of chrysemyd turtles as well.

Mensural characters were converted to proportions to evaluate differences in shape among chrysemyd species. The analysis of ratios was univariate,

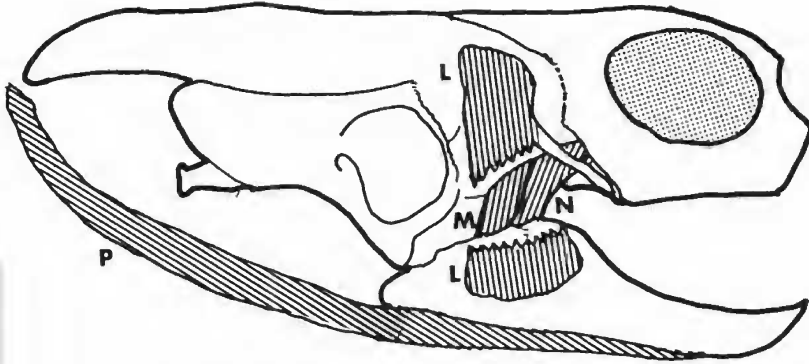


FIG. 3.—Diagrammatic representation of the skull and cranial muscles of a generalized chrysemid, in lateral view, with zygomatic arch, adductor mandibularis externus and internus, adductor mandibularis anterior and posterior removed: L, adductor mandibularis medialis (center section removed); M, pterygoideus Pars dorsalis; N, pterygoideus Pars ventralis; P, branchiomandibularis.

and the means were tested for significant differences by the Students' *t* at a 95 per cent confidence level.

Specimens were examined as follows: SKULL, *Chrysemys picta* (42); *Pseudemys alabamensis* (6); *P. concinna* (64); *P. floridana* (35); *P. nelsoni* (23); *P. rubriventris* (10); *P. texana* (23); *Trachemys scripta* (75). CARAPACE, *Chrysemys picta* (114); *Pseudemys alabamensis* (26); *P. concinna* (217); *P. floridana* (118); *P. nelsoni* (31); *P. rubriventris* (9); *P. texana* (51), *Trachemys scripta* (1199). MUSCLES, *Chrysemys picta* (7); *Pseudemys concinna* (12); *P. floridana* (5); *P. nelsoni* (6); *P. texana* (13); *Trachemys scripta* (18).

The specimens derive from the Academy of Natural Sciences, Philadelphia (ANSP); American Museum of Natural History, New York; Auburn University, Auburn; British Museum (Natural History), London; Florida State Museum, Gainesville; Museum of Natural History, University of Kansas, Lawrence (KU); University of Michigan Museum of Zoology, Ann Arbor (UMMZ); University of Missouri, Columbia; Museum of Comparative Zoology, Harvard University, Cambridge (MCZ); Texas Cooperative Wildlife Collection, Texas A&M University, College Station (TCWC); The Museum of Texas Tech University, Lubbock (TTU); Tulane University, New Orleans; Turtle Run Research Institute, Panama City, Florida; United States Museum of Natural History, Washington; University of Texas-Arlington Collection, Arlington (UTACV-R); University of Utah, Salt Lake City (UU).

RESULTS AND DISCUSSION

Cranial Observations

Mensural features of the skull and mandible provide reliable systematic indicators in chrysemid turtles. Thirty-four measurements represented by 36 ratios were used to verify relationships among populations (Table 1), but

only 20 of those ratios will be discussed. The 20 ratios analyze 21 mensural features that quantify subjective observations of seven aspects of the skull. Those aspects include: skull profile, nasal aperture, temporal fossa, and pterygoid elements; the arches; the upper jaw; and the mandible and lower alveolar shelf. Analysis of characters is by reference to populations (arbitrarily termed *alabamensis*, *concinna*, *floridana*, *nelsoni*, *picta*, *rubriventris*, *scripta*, and *texana*, without regard to current taxonomic status), which will be defined later herein.

The skulls of chrysemyds are superficially quite similar, but closer scrutiny reveals several major differences among populations. Sexual dimorphism in skull shape is well developed in most populations, except *concinna* and *floridana*, which show few sexually dimorphic features, or *picta*, which lacks apparent dimorphism. Sexual dimorphism is manifested in more gracile shaped skulls in males than in females.

In profile, the skull has a gradual vertical rise from the prefrontal to the supraoccipital crest, although in *scripta* the rise is very steep, whereas the skulls of *concinna* and *floridana* are flat, with little rise. Chrysemyds have highly vaulted skulls compared to most other emydines, the skull height (ho)/bc ranging from 0.36 to 0.41, except *picta* which has a low skull roof despite its perceptible rise (ho/bc = 0.34). The highly vaulted skull is considered a derived character in chrysemyds.

The interorbital areas in chrysemyds are about the same size relative to basiocranial length in all populations (io/bc = .20-.21) except in *concinna* and *floridana*, which are slightly broader (io/bc = .22). However, the nasal aperture is relatively small in *picta* [nares width (wn)/bc is about 0.15] compared to the other populations (mean range wn/bc 0.17-0.19), except in *concinna* (0.21).

Relative to length, the chrysemyd skulls are wide, skull width (wa)/bc ranges between 0.72 and 0.73. The exception is *picta*, which has a narrow skull (wa/bc = 0.69). The narrower skull in *picta* also is reflected in the narrow temporal fossa (temporal fossa width (we)/length (le) = 0.45) compared to the other populations in which the width is half the length. Conversely, the pterygoids are much broader in *picta* (wp/wa = 0.36) than in the other populations, which are more nearly like the ancestral form in this feature, or the pterygoid width (wp) is about 30 per cent of the skull width (wa). Female chrysemyd skulls are broader (wa/bc = 0.74) than those of males (wa/bc = 0.72) in most populations except *picta*, *concinna*, and *floridana*.

Skull shape within the chrysemyds then varies from low and narrow (*picta*) to vaulted and wide (*texana*). This variation correlates to jaw structure, which is discussed later. Likely the narrow, low skull is a primitive character in chrysemyds and in emydines in general (Ward, 1980).

Well-developed arches, composed of broad, flat elements, characteristic of emydines (Ward, 1980), are epitomized in the chrysemyds. Because of the uniformity of their sizes relative to basiocranial length within populations,

TABLE 1.—Selected ratios from skull measurements in chrysemyd turtles. Numbers in table are ratios times 100, means \pm standard deviation; see text for abbreviations.

Variate	pirita 41	scripta 58	concinna 63	floridana 33	alabamensis 6	nelsoni 20	rubriventris 10	texasia 23
wpo/bc	12.8 \pm 1.5	14.7 \pm 1.7	18.1 \pm 1.7	18.2 \pm 1.8	14.7 \pm 1.3	18.5 \pm 1.7	14.0 \pm 1.9	17.9 \pm 1.9
wj/bc	6.5 \pm 1.3	8.9 \pm 1.9	11.7 \pm 1.4	11.9 \pm 1.1	11.8 \pm 0.2	11.9 \pm 1.5	11.8 \pm 0.8	10.1 \pm 1.4
wz/bc	20.2 \pm 2.2	20.5 \pm 2.4	24.0 \pm 2.4	26.5 \pm 2.5	24.9 \pm 1.2	26.2 \pm 2.0	26.0 \pm 1.6	25.2 \pm 2.2
hmx/bc	9.1 \pm 1.1	11.8 \pm 1.4	13.8 \pm 1.2	14.2 \pm 1.1	15.7 \pm 0.8	14.0 \pm 1.4	13.8 \pm 1.7	13.0 \pm 1.3
hpm/bc	8.9 \pm 1.7	10.7 \pm 1.4	10.3 \pm 1.2	11.2 \pm 0.9	12.2 \pm 1.3	12.4 \pm 1.8	13.0 \pm 1.7	11.3 \pm 0.9
wmxpo/bc	55.2 \pm 2.7	58.5 \pm 2.5	60.9 \pm 2.2	61.5 \pm 2.7	65.4 \pm 1.5	61.2 \pm 2.3	60.6 \pm 2.1	59.8 \pm 3.2
wa/bc	68.7 \pm 3.3	73.1 \pm 3.2	72.4 \pm 3.4	72.2 \pm 2.4	75.3 \pm 1.8	72.6 \pm 3.7	72.1 \pm 2.9	73.0 \pm 3.6
ho/bc	34.2 \pm 1.4	37.5 \pm 1.4	40.5 \pm 2.2	40.9 \pm 1.7	36.7 \pm 0.7	38.1 \pm 1.8	36.2 \pm 2.4	38.6 \pm 1.8
ao/bc	49.1 \pm 2.3	47.3 \pm 1.9	49.4 \pm 2.0	50.0 \pm 1.3	52.2 \pm 1.6	49.5 \pm 2.5	49.2 \pm 1.8	50.3 \pm 1.8
io/bc	20.5 \pm 1.3	19.5 \pm 1.8	22.7 \pm 1.9	21.6 \pm 2.2	20.0 \pm 1.2	21.0 \pm 1.5	20.4 \pm 2.6	19.3 \pm 1.6
wmxo/bc	13.2 \pm 1.3	17.6 \pm 1.7	19.2 \pm 1.4	18.8 \pm 1.5	24.1 \pm 1.0	22.3 \pm 1.5	21.7 \pm 1.6	21.8 \pm 1.2
lmsa/bc	64.1 \pm 2.5	70.7 \pm 2.7	64.3 \pm 2.0	65.9 \pm 2.2	67.6 \pm 0.7	66.7 \pm 2.0	67.1 \pm 1.1	66.7 \pm 1.5
th/bc	6.9 \pm 0.9	6.7 \pm 0.7	7.9 \pm 0.6	7.9 \pm 0.8	8.7 \pm 0.8	8.4 \pm 0.5	7.8 \pm 1.1	7.9 \pm 0.6
wtm/bc	10.4 \pm 0.3	12.0 \pm 0.3	13.9 \pm 0.4	12.1 \pm 0.2	19.3 \pm 0.1	17.7 \pm 0.1	17.2 \pm 0.1	17.7 \pm 1.4
le/lso	62.7 \pm 1.7	63.2 \pm 1.7	61.4 \pm 1.9	60.2 \pm 1.2	64.2 \pm 2.3	60.5 \pm 1.8	61.1 \pm 1.2	63.0 \pm 2.2
we/le	44.7 \pm 3.5	49.9 \pm 2.8	47.4 \pm 3.5	48.5 \pm 4.9	48.5 \pm 2.3	49.2 \pm 6.2	51.1 \pm 2.2	55.9 \pm 6.8
ws/lo	56.9 \pm 6.3	66.8 \pm 10.8	58.0 \pm 7.4	57.6 \pm 11.6	70.8 \pm 4.8	67.7 \pm 7.4	66.3 \pm 7.0	65.1 \pm 3.8
wp/wa	35.6 \pm 2.5	32.6 \pm 2.3	30.5 \pm 3.0	31.3 \pm 1.9	25.2 \pm 2.1	27.2 \pm 2.3	27.2 \pm 2.3	32.3 \pm 2.4
hpm/hmx	98.3 \pm 19.7	92.0 \pm 14.0	75.4 \pm 8.3	79.2 \pm 6.9	78.4 \pm 12.1	88.8 \pm 12.6	94.4 \pm 13.6	88.3 \pm 11.8
wmxs/wtmx	76.0 \pm 11.8	64.3 \pm 9.9	68.7 \pm 7.3	68.9 \pm 6.9	87.3 \pm 6.0	97.2 \pm 15.6	96.8 \pm 18.7	83.5 \pm 10.9
lmsj/lmsa	63.5 \pm 4.1	58.1 \pm 2.7	64.3 \pm 3.1	63.3 \pm 2.8	64.7 \pm 2.9	63.0 \pm 3.2	62.1 \pm 1.3	61.5 \pm 2.9
wma/lmsa	96.7 \pm 4.3	94.1 \pm 4.2	102.9 \pm 6.6	98.5 \pm 4.5	98.2 \pm 3.5	97.4 \pm 4.7	99.2 \pm 4.9	100.2 \pm 3.6
hc/lmsa	30.0 \pm 2.0	31.5 \pm 2.7	32.2 \pm 2.9	30.5 \pm 1.7	29.3 \pm 1.6	27.7 \pm 1.9	27.3 \pm 1.8	29.7 \pm 1.4
wtm/lmsa	16.2 \pm 0.1	17.0 \pm 0.1	21.6 \pm 0.2	18.3 \pm 0.1	28.5 \pm 0.1	26.6 \pm 0.1	25.9 \pm 0.1	26.5 \pm 1.9
wmj/wma	82.5 \pm 3.1	81.1 \pm 2.9	91.3 \pm 3.3	83.4 \pm 3.5	86.6 \pm 4.0	82.0 \pm 3.9	79.6 \pm 3.7	80.6 \pm 2.8
wtm/ws	56.9 \pm 7.5	63.0 \pm 9.1	82.9 \pm 8.8	72.8 \pm 6.8	92.9 \pm 6.3	84.1 \pm 4.4	89.5 \pm 9.7	89.0 \pm 8.6
wtm/hc	54.0 \pm 7.0	54.0 \pm 5.0	67.0 \pm 7.0	60.0 \pm 8.0	97.2 \pm 8.5	96.0 \pm 9.0	94.9 \pm 4.7	89.5 \pm 8.1

and their variation between populations, the arches (jugal, postorbital, and zygomatic) are useful taxonomic indicators. The zygomatic arch width (wz) is the greatest of the three arches, over 25 per cent of the basiocranial length in most populations, although only 20 in *picta* and *scripta*. The postorbital arch width (wpo) is about 18 per cent of the basiocranial length, except in *picta* (13%), *rubriventris* (14%), *alabamensis*, and *scripta* (15%). More substantial interpopulational differences in jugal arch width (wj) occur. The jugal arch is about 12 per cent of the basiocranial length in most chrysemyds except *picta* (6%) and *scripta* (9%). The differences in arch size reflect divergence in feeding habits and differences in cranial musculature (Ward, 1980).

The maxillary and premaxillary components of the tomial ridge are buttressed by the amount of bone between the edge of the ridge and the orbit or the nasal aperture. The presence of tomiodonts is adduced by the relative sizes of the premaxilla (hpm) compared to the maxilla (hmx). With the presence of tomiodonts, the ratio hpm/hmx might be expected to approximate unity (1.0) or greater, whereas the lack of tomiodonts should be indicated by a ratio much less than one. Tomiodontation is found in *alabamensis*, *nelsoni*, *picta*, *rubriventris*, and *texana*, but not in *concinna*, *floridana*, or *scripta*. As expected, hpm/hmx in *picta* is 0.98, but in no population does the ratio exceed 1.0. The ratios in *alabamensis* (0.78), *nelsoni* (0.89), *rubriventris* (0.94), and *texana* (0.88) contradict the expected results. Based on this evidence, it is plain that an hpm/hmx ratio of about 0.90 more accurately indicates the presence of tomiodonts. The reason becomes more evident when the ratios hpm/bc and hmx/bc are compared. The maxilla and the premaxilla are both small in *picta* ($hmx/bc = 0.09$; $hpm/bc = 0.09$) compared to the other populations, although in every other population the maxillary component is much larger than that of the premaxilla. With the modification of the premaxilla into tomiodonts, the base structure is reduced proportionally to the size of the tomiodonts, resulting in comparably equivalent sizes of the overall component although the base premaxilla (without the tomiodonts) is much smaller than the maxilla. The maxillary component is actually larger, providing support for the crushing surface of the jaw. Tomiodonts are not projecting outgrowths but, rather, result from an erosion of the basal elements, leaving the toothlike structure.

Returning to the ratios, hpm/hmx , found in *alabamensis* (0.78), *concinna* (0.75), and *floridana* (0.79), the results appear to contradict even the revised hypothesis (hpm/hmx of about 0.90 indicates tomiodonts). However, my sample of *alabamensis* consists mainly of very large females that have extremely thick maxillae. The hmx/bc is 0.16 in *alabamensis*, 0.14 in *concinna* and *floridana*, 0.13 to 0.14 in *nelsoni*, *rubriventris* and *texana*, 0.12 in *scripta*, and 0.09 in *picta*. The premaxillary components of those same populations are: 0.12, 0.10, 0.11, 0.12, 0.13, 0.11, 0.11, and 0.09, respectively. In fact, *texana* is the only population that does not have the

expected ratio hpm/hmx compared to the other populations with tomiodonts. The tomiodentition in *texana* is reduced in size relative to similar-sized specimens of *alabamensis*, *nelsoni*, or *rubriventris*.

The upper jaw provides a strong inertial base to support the crushing action when the mandible is addressed. As such, it reflects the modifications in surface contours found on the lower jaw, although not as a mirror image. The upper alveolar shelf width ($wmxo$) is about 25 per cent greater than the lower alveolar shelf width (wtm) except in *concinna* (38%), *floridana* (55%) and *scripta* (46%). The median ridge is strongly cusped in several populations (*alabamensis*, *nelsoni*, *rubriventris*, *texana*), less so in *concinna* and *floridana*, but only slightly cusped in *picta* or *scripta*.

The upper alveolar shelf is very wide ($wmxo/bc = 0.21-0.24$) in four populations, and slightly less (0.19) in *concinna* and *floridana*, whereas in *scripta* (0.17) and *picta* (0.13) it is narrow. The upper jaw width ($wmxpo$) reflects the alveolar shelf width and, to a lesser extent, the skull width in chrysemyds. As shown before, *picta* has a narrow skull, narrow jaw ($wmxpo/bc = 0.55$) and narrow alveolar shelf compared to the other populations ($wmxpo/bc = 0.60-0.65$). However, *scripta* jaw width ($wmxpo/bc = 0.58$) and alveolar shelf width fall between *picta* and the remaining populations, although the skull in *scripta* is relatively wider than in *concinna* or *floridana*.

The length of the lower jaw ($lmsa$) compared to the basiocranial length (bc) varies between populations from 0.64 in *picta* and *concinna*, 0.66 in *floridana*, 0.67 to 0.68 in *alabamensis*, *nelsoni*, *rubriventris*, and *texana*, to 0.71 in *scripta*. Comparing the width of the mandible (wma) to its length, *scripta* (0.94) has a long, narrow jaw and *concinna* (1.03) a short, wide jaw, whereas the remaining populations have jaws intermediate in dimensions (0.97-0.99).

The lower alveolar shelf width has greater variation among populations of chrysemyds than any other single structure. The wide lower shelf reflects the upper alveolar shelf width but is more strongly cusped than is the upper shelf. The number of primary cusps on each mandible varies from two in *picta* and *scripta*, four in *concinna* and *floridana*, to six in the other populations. The additional cusping is accompanied by widening of the shelf. Wider shelves require stronger support elements.

When the thickness of the mandibular ramus at the coronoid (th) is compared to basiocranial length, the results confirm that *scripta* and *picta* ($th/bc = 0.07$) have relatively thin rami supporting narrow alveolar shelves, whereas the other populations have thicker rami ($th/bc = 0.08$) that support wider shelves. The ratio of the alveolar shelf width (wtm) to the mandible length ($lmsa$) provides a point of reference to account for the thinner ramus support found in *picta* and *scripta*. The $wtm/lmsa$ for *picta* (0.16) and *scripta* (0.17) are small compared to those of *floridana* (0.18), *concinna* (0.22), *rubriventris* (0.26), *texana* (0.26), *nelsoni* (0.27), and *alabamensis* (0.28). This wide shelf is further demonstrated by comparing the alveolar

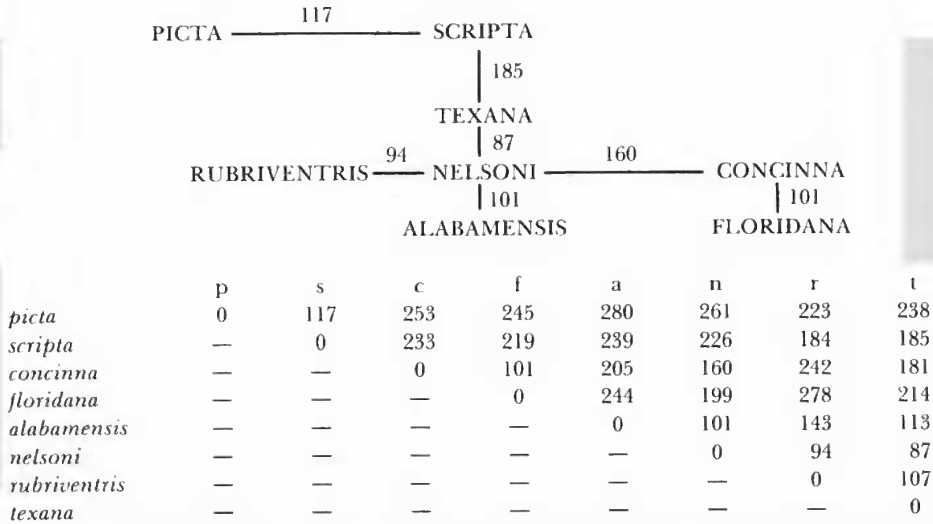


FIG. 4.—Shortest distance network of patristic distances derived from 35 cranial ratios between chrysemys populations. See Table 1 for cranial ratios used. Methodology of Zug (1973).

shelf width to the symphyseal length (ws): *picta* (0.57), *scripta* (0.63), *floridana* (0.73), *concinna* (0.83), *nelsoni* (0.83), *texana* (0.89), *rubriventris* (0.90), and *alabamensis* (0.93).

Comparing the lower alveolar shelf width to the basiocranial length further elucidates the disparity in shelf size between populations. The narrow shelf of *picta* ($wm/bc = 0.10$) and *scripta* (0.12) is surprisingly matched by that of *floridana* (0.12). The remaining populations are substantially broader, wm/bc ranging from 0.14 in *concinna* to 0.19 in *alabamensis*, although *nelsoni* (0.18), *rubriventris* (0.17), and *texana* (0.18) have much broader shelves than *concinna*. Further comparison of the shelf width to the coronoid height (hc), which is about 30 per cent of the mandible length in chrysemys, provides more evidence of the wider jaw surface in *alabamensis*, *nelsoni*, *rubriventris*, and *texana* ($wm/bc = 0.85-0.97$) than in *picta* or *scripta* (0.54), or in *floridana* (0.60) and *concinna* (0.67). The wider alveolar shelves are derived from a primitive narrow shelf characteristic of the emydine ancestral form.

A species similarity matrix of patristic distances derived from the 35 cranial ratios break into four species groups (Fig. 4). These groups are separated by distances of 115 or more, whereas populations within groups are separated by less than 101. From the matrix, the following species groups are evident within the chrysemys: 1) *picta*, 2) *scripta*, 3) *floridana* (*concinna* and *floridana*), 4) *rubriventris* (*alabamensis*, *nelsoni*, *rubriventris*, *texana*). Species groups are listed in order of nomenclatural priority rather than by any presumption of phylogenetic relationships.

The distance from *picta* to the nearest *rubriventris* complex population (*rubriventris*) is 223, but the mean distance from *picta* to the *rubriventris*

complex is 250 (average of all populations within the complex) and to the *floridana* complex the mean is 249. The mean distance from *scripta* to the *rubriventris* complex is 208, and to the *floridana* complex is 226. The mean distance between the *floridana* complex and the *rubriventris* complex is 215, although the shortest distance is 160 (between *concinna* and *nelsoni*). Within the *rubriventris* complex, the mean distance between populations is 107, yet between *alabamensis* and *nelsoni*, *nelsoni* and *rubriventris*, *nelsoni* and *texana*, and *rubriventris*, the distances are 101, 94, 87, and 107, respectively. The distance between *concinna* and *floridana* is 101.

Of the 35 ratios considered, *picta* is significantly different from *scripta* in 29, and from the pseudemyds (the *floridana* complex and the *rubriventris* complex collectively) in 23 ratios. The *scripta* population is significantly different from the pseudemyds in 22 ratios. Differences in 11 ratios are found between all three groups (*picta*, *scripta*, and the pseudemyds).

The *floridana* complex is significantly different from the *rubriventris* complex in 16 ratios. Populations within the *rubriventris* complex vary significantly in 7 to 10 ratios (Table 2), but in no single ratio are all four *rubriventris* populations significantly different from each other. In fact, only in four ratios are any three populations within the *rubriventris* complex significantly different from each other.

All populations within the *floridana* complex share characteristics of relative skull height, upper and lower alveolar shelf widths, mandible thickness, and pterygoid width. The slight anterior narrowing of the alveolar shelf is reflected in the ratio of the anterior width (w_{tms}) to the posterior width (w_{tmo}) of the upper alveolar shelf (in both *concinna* and *floridana* $w_{tms}/w_{tmo} = 0.69$). The relative width of the upper alveolar shelf to the basiocranial length is 0.19 in both, but the width of the lower alveolar shelf to the mandible length is 0.22 in *concinna* and 0.18 in *floridana*.

Members of the *rubriventris* complex have relatively higher premaxillary elements ($h_{pm}/bc = 0.11-0.13$) than does the *floridana* complex, or do *picta* and *scripta*. The *rubriventris* complex also has wider alveolar shelves ($w_{tm}/l_{msa} = 0.26-0.29$), longer mandibles ($l_{msa}/bc = 0.67-0.68$, except for the 0.71 of *scripta*), and greater cusping (mean of six cusps on the mandible compared to four cusps in the *floridana* complex and two cusps in *picta* and *scripta*).

The pseudemyds are distinguished by jugal arch widths ($w_j/bc = 0.10-0.12$), wide zygomatic arches ($w_z/bc = 0.24-0.26$), skull widths ($w_a/bc = 0.72+$), and otic capsule length ($ao/bc = 0.49-0.52$).

Other, more subjective, osteological features of the cranium separate populations. The postorbital arch width is subequal to the length of the orbit in the pseudemyds, whereas it is always smaller than the orbit in *picta* or *scripta*. The prootic contribution to the temporal shelf is only a sliver in *picta* compared to that in other populations. The groove on the internal pterygoid process in which lies the pars ventralis of the pterygoideus muscle

TABLE 2.—Significant differences of the means (at 95% confidence level) between populations of *chrysemys* skull measurement ratios. Plus sign indicates significant difference; 0, not significant; populations compared are identified by first letter of name; see text for abbreviations.

Variate	p:n	pt	pf	ps	s:n	sc	sl	cl	nc	nl	na	nt	nt	ar	at	rt
wpo/bc	+	+	+	+	+	+	+	0	0	0	+	+	0	0	+	+
wj/bc	+	+	+	+	+	+	+	0	0	0	0	0	0	0	0	0
wz/bc	+	+	+	0	+	+	+	0	0	0	0	0	0	0	0	0
hmx/bc	+	+	+	+	+	+	+	0	0	0	+	0	+	+	+	0
hpm/bc	+	+	+	+	+	0	0	+	+	+	0	0	0	0	0	0
wmxpo/bc	+	+	+	+	+	+	+	0	0	0	+	0	0	+	+	0
wa/bc	+	+	+	+	0	0	0	0	0	0	0	0	0	0	0	0
ho/bc	+	+	+	+	+	+	+	0	+	+	0	0	0	0	0	0
ao/bc	0	0	0	+	+	+	+	0	0	0	0	0	0	0	0	0
io/bc	0	+	+	+	+	+	+	+	+	0	0	0	0	0	0	0
wtmxo/bc	+	+	+	+	+	+	+	0	+	+	+	0	0	+	+	0
lmsa/bc	+	0	+	+	+	+	+	+	+	+	0	0	0	0	0	0
th/bc	+	+	+	0	+	+	+	0	+	+	0	+	0	+	0	0
wtm/bc	+	+	+	+	+	+	0	+	+	+	0	0	0	+	0	0
le/lso	+	+	+	+	+	+	+	+	0	0	+	0	0	+	+	0
we/le	+	+	+	+	0	+	0	0	0	0	0	0	0	0	0	0
ws/lo	+	0	0	+	0	+	+	0	+	+	0	0	0	0	0	0
wp/wa	+	+	+	+	+	+	+	0	+	+	0	0	+	0	+	+
hpm/hmx	0	+	+	+	0	+	+	+	+	+	0	0	0	0	0	0
wtmxs/wtmxo	+	+	+	+	+	+	+	0	+	+	0	0	0	0	0	0
lmsj/lmsa	0	0	0	+	+	+	+	0	0	0	0	0	0	0	0	0
wma/lmsa	0	+	0	+	+	+	+	+	+	0	0	0	0	0	0	0
hc/lmsa	+	+	0	+	+	0	0	0	+	+	0	0	+	0	0	+
wtm/lmsa	+	+	+	+	+	+	+	+	+	+	+	+	+	0	0	0
wmj/wma	0	+	0	+	+	+	+	+	+	0	+	0	0	+	+	+
wtm/ws	+	+	+	+	+	+	+	+	0	+	+	+	+	0	0	0
wtm/hc	+	+	+	0	+	+	+	+	+	+	0	0	+	0	+	+

is shallow in *scripta*, whereas it is very deep in the other populations. The posterior extent of the palatine is at the level of the external pterygoid process in pseudemyds, just anterior to it in *picta*, and well anterior in *scripta*. The columella extends from the quadrate to the jugal in *scripta* and the pseudemyds, whereas in *picta* the columella is smaller and does not extend to the jugal (Monks, 1878). Only *picta* lacks a medial ridge on the mandible. The symphyseal ridge is well developed in the pseudemyds, only slightly in *scripta*, but not at all in *picta*. The anterior edge of the mandible at the symphysis turns abruptly dorsally in the pseudemyds, forming nearly a right angle, whereas in *picta* and *scripta* it curves up more gradually. Only *picta* lacks a lingual shelf (Ward, 1980). The lateral ridge in the pseudemyds is serrated (very strongly in the *rubriventris* complex) but not in either *picta* or *scripta*. The pseudemyds have prominent cusps on the mandible, whereas the cusps are low and often indistinguishable in *picta* or *scripta*. The external fossa is very deep in *scripta* compared to the other groups.

The palatine contributes 30 to 35 per cent of the upper alveolar shelf in the *floridana* complex and in *picta*, whereas it contributes 40 to 45 per cent of the shelf in the *rubriventris* complex and in *scripta*. There are two well-defined fossae in the palatal shelf in the *floridana* complex, whereas none is found in *picta* or *scripta*, and only slight depressions are found in the *rubriventris* complex. Tomiodonts are not found in *scripta* or the *floridana* complex (except in some *concinna*, particularly those west of the Mississippi River) but occur in *picta* and are well developed in the *rubriventris* complex. The ventral edge of the tomium is straight in *picta* and *scripta*, whereas it rises slightly dorsally at the anterior extent in the *floridana* complex and rises posteriorly in the *rubriventris* complex. There is extensive sexual dimorphism in the skulls of *scripta* and the *rubriventris* complex, very little in the *floridana* complex and none at all in *picta*. The supraoccipital crest is relatively longer in proportion to the skull length in the *floridana* complex than in the other groups. The occipital condyle and the temporal shelf extend farther posteriorly beyond the articular condyles in the *floridana* complex than in the other groups. The posterior edge of the vomer ends well anterior to the posterior edge of the palatine in *picta* and in the *floridana* complex, whereas in *scripta* and the *rubriventris* complex the vomer and the palatine extend equally far posteriorly. Neither the angular nor the prearticular elements extend anteriorly beyond the coronoid in the *floridana* complex, but both extend beyond the coronoid in the *rubriventris* complex. The angular extends beyond the coronoid in *scripta*, but the prearticular does not, and in *picta*, the prearticular does not extend beyond the coronoid, but the angular extends at least to the level of the coronoid.

Chrysemyd turtles share cranial muscle features with other emydines; in fact, with a few notable exceptions, the same muscle groups are found throughout the subfamily. As a group, chrysemyd populations all have six of nine major muscle groups that are present in emydines. Additionally, one major muscle is present in three of four species groups and the other two major muscles are found in at least two of the four species groups. Of 13 distinct muscles dissected, all are found within the chrysemyds (Table 3), although no single species group has all 13 muscles. Seven of these muscles are noticeably enlarged in at least one chrysemyd population.

Two populations, *concinna* and *floridana*, differ in myology in only one aspect—the pars medius of the adductor mandibularis externus is absent in *floridana* but not in *concinna*. The *floridana* complex has two muscles, intramandibularis and zygomaticomandibularis, that are not found in the *rubriventris* complex. The intramandibularis also is absent in *picta*, and the zygomaticomandibularis is absent in *scripta*. The adductor mandibularis anterior is found in the *rubriventris* complex and in *scripta* but not in *picta* or the *floridana* complex. The adductor mandibularis medialis is not separable in *picta* but is found in each of the other populations and is enlarged in *scripta* compared to the pseudemyds. The pars medius is greatly

TABLE 3.—Cranial muscle groups found in chrysemyd turtles. Zero indicates that a muscle is absent; 1, muscle present; 2, that the muscle is enlarged relative to other cranial muscles when compared to other populations; 3, greatly enlarged. Populations represented are Cp, *picta*; Pc, *concinna*; Pf, *floridana*; Pn, *rubriventris* complex; Ts, *scripta*.

Muscle	Cp	Pc	Pf	Pn	Ts
Adductor mand. externus	2	1	1	1	1
Pars profundus	2	1	1	1	1
Pars superficialis	2	1	1	1	1
Pars medius	1/0	0	1	3	3
Adductor mand. internus	1	2	2	1	2
Pseudotemporalis	1	1	1	1	1
Intramandibularis	0	1	1	0	1
Adductor mand. anterior	0	0	0	1	1
Adductor mand. posterior	1	1	1	1	1
Adductor mand. medialis	0	1	1	1	2
Pterygoideus	1	2	2	1	1
Pars dorsalis	3	1	1	1	1
Pars ventralis	1	2	2	1	1
Zygomandibularis	1	1	1	0	0
Depressor mandibularis	1	1	1	1	1
Branchiomandibularis	2	2	2	2	1

enlarged in *scripta* and the *rubriventris* complex as compared to *picta* or the *floridana* complex. However, the adductor mandibularis externus is a larger muscle mass in *picta* than in the other populations. The pterygoideus is a larger muscle in the *floridana* complex than in the other populations.

The cranial muscle evidence separates *picta* from the other populations by a large margin of difference. Additionally, the *floridana* complex is greatly different from either the *rubriventris* complex or *scripta* relative to cranial myology. There are few major differences between *scripta* and the *rubriventris* complex in cranial muscles.

Shell morphology has limited taxonomic utility (Gaffney, 1972). Some authors have placed considerable emphasis on the taxonomic usefulness of ratios or direct comparisons of measurements of scute or bony element dimensions (Milstead, 1969; Weaver and Robertson, 1967; Rose and Weaver, 1966). The lengths of the vertebral scutes relative to carapace length are remarkably uniform throughout the chrysemyds but, with exception of *picta*, have little taxonomic value. Vertebrals I and II are longer in *picta* ($vI/cl = 0.19$; $vII/cl = 0.21$) compared to other populations (0.16-0.17; 0.18-0.19) whereas vertebrals IV and V are shorter in *picta* (0.17 and 0.16) than in other populations (both 0.18-0.20). The interpleural scute seam lengths relative to carapace height have more striking differences among populations but with greater intrapopulation variation (Table 4). Plastral interscute seam lengths, when compared to plastron length, particularly the interhumeral seam (0.14 in *scripta*; 0.16-0.18 in others) and the interfemoral seam (0.13-0.14 in *floridana* and *concinna*; 0.09-0.13 in other populations)

TABLE 4.—Ratios of measurements from shells of chrysemyd turtles. Numbers in table are ratios times 100, means \pm standard deviations, rounded to nearest whole integer. Abbreviations are: *cl*, carapace length; *cw*, carapace width; *ch*, carapace height; *pll*, plastron length; *apw*, width of anterior plastral lobe; *ppw*, width of posterior plastral lobe; *gul*, intergular seam length; *hum*, interhumeral seam length; *pec*, interpectoral seam length; *abd*, interabdominal seam length; *fem*, interfemoral seam length; *an*, interanal seam length; *nl*, length of dorsal portion of cervical scute; *nw*, width of dorsal portion of cervical scute; *vw*, width of ventral portion of cervical scute; *vl*, length of ventral portion of cervical scute; *V₂*, length of second vertebral scute; *V₄*, height of third pleural scute measured along seam between third and fourth pleural scute. Species are *Pc*, *Pseudemys concinna*; *Pf*, *Pseudemys floridana*; *Pn*, *Pseudemys nelsoni*; *Pt*, *Pseudemys texana*; *Ts*, *Trachemys scripta*; *Cp*, *Chrysemyd picta*; number in parentheses.

Variate	<i>Pc</i> (40)	<i>Pf</i> (25)	<i>Pn</i> (18)	<i>Pt</i> (30)	<i>Ts</i> (50)	<i>Cp</i> (16)
<i>cw/cl</i>	73 \pm 4	75 \pm 4	71 \pm 3	73 \pm 2	74 \pm 4	76 \pm 3
<i>ch/cl</i>	37 \pm 3	43 \pm 2	44 \pm 4	38 \pm 3	40 \pm 3	36 \pm 3
<i>ch/cw</i>	50 \pm 4	60 \pm 5	62 \pm 3	52 \pm 4	54 \pm 5	47 \pm 4
<i>pll/cl</i>	88 \pm 3	89 \pm 3	90 \pm 4	87 \pm 3	92 \pm 4	94 \pm 3
<i>apw/ppw</i>	94 \pm 4	101 \pm 5	98 \pm 3	89 \pm 4	96 \pm 4	90 \pm 4
<i>gul/pll</i>	16 \pm 1	16 \pm 1	18 \pm 1	15 \pm 1	18 \pm 2	20 \pm 1
<i>hum/pll</i>	8 \pm 1	7 \pm 1	10 \pm 1	8 \pm 1	8 \pm 3	7 \pm 1
<i>pec/pll</i>	16 \pm 2	18 \pm 1	16 \pm 1	17 \pm 1	14 \pm 2	13 \pm 2
<i>abd/pll</i>	27 \pm 2	27 \pm 2	30 \pm 1	28 \pm 2	27 \pm 2	24 \pm 4
<i>fem/pll</i>	14 \pm 2	13 \pm 3	9 \pm 1	13 \pm 2	13 \pm 2	10 \pm 3
<i>an/pll</i>	20 \pm 1	20 \pm 1	19 \pm 1	20 \pm 2	22 \pm 2	23 \pm 3
<i>nl/cl</i>	6 \pm 1	7 \pm 2	8 \pm 1	8 \pm 1	8 \pm 1	10 \pm 1
<i>nw/cw</i>	4 \pm 1	7 \pm 1	4 \pm 1	3 \pm 1	4 \pm 1	6 \pm 1
<i>vw/nw</i>	145 \pm 45	85 \pm 11	125 \pm 18	159 \pm 28	138 \pm 21	111 \pm 12
<i>vl/nl</i>	32 \pm 10	43 \pm 9	59 \pm 5	32 \pm 3	94 \pm 15*	77 \pm 9
<i>V₂/cl</i>	18 \pm 2	18 \pm 1	19 \pm 2	18 \pm 1	18 \pm 1	21 \pm 3
<i>V₄/cl</i>	19 \pm 3	20 \pm 1	20 \pm 1	19 \pm 2	19 \pm 1	17 \pm 1
<i>P₁/ch</i>	64 \pm 5	57 \pm 3	59 \pm 4	61 \pm 4	60 \pm 4	63 \pm 7
<i>P₃/ch</i>	47 \pm 8	43 \pm 5	43 \pm 2	41 \pm 5	43 \pm 6	47 \pm 7

*The large deviation resulted from a split with half the specimens with a mean of 110 \pm 7 and the other half 83 \pm 4, without regard to sex or size or subspecies.

distinguish chrysemyds. The shape of the cervical scute is a reliable feature that separates certain populations.

The very wide dorsal cervical scute of *floridana* (cervical width (*nw*)/carapace width = 0.07) and *picta* (0.06) compared to other populations (0.03-0.05) and the relatively long dorsal cervical in *nelsoni* and *texana* (*nl/cl* = 0.08) compared to that in other populations (0.06), except *picta* (0.10), is a useful taxonomic aid. Similarly, the length of the ventral cervical scute compared to the dorsal cervical scute is a remarkably clear differentiator of populations (0.33 in *concinna*, 0.43 in *floridana*, 0.59 in *nelsoni*, 0.77 in *picta*). Weaver and Rose (1967) used a similar measurement but compared the ventral cervical scute to the nuchal bone length (nuchal scute underlap).

The posterior marginals are strongly notched in *scripta*, slightly so in the pseudemyds, and not at all in *picta*. Shell shape seems correlated to habitat and in some cases separate populations. However, significant differences in

shell proportions are found only between *concinna* and *picta* and not between all populations. Nonetheless, some distinguishing features are found. The shell height compared to length indicates that *picta* (0.36), *concinna* (0.37) and *texana* (0.38) have low vaulted shells relative to *scripta* (0.40) and the other populations (0.43-0.44). Carapace width relative to length ranges from 0.71 in *nelsoni*, *rubriventris* and *alabamensis*; 0.73 in *concinna*, *floridana*, and *texana*; 0.74 in *scripta*; to 0.76 in *picta*. Plastron lengths compared to carapace lengths range from 0.87-0.90 in the pseudemyds, 0.92 in *scripta* and 0.94 in *picta*.

Extensive shell rugosity occurs in all pseudemyds and *scripta*, except that *floridana* complex adults have only shallow rugosity, particularly those from the more northern Atlantic coastal communities. No rugosity is found in *picta*. Only *scripta* has a strong keel on the first vertebral.

The free portions of ribs 2-4 compared as to length show considerable variation interspecifically. The second rib is longest and the fourth shortest in *concinna*, *floridana* and *scripta*. In *picta*, the third is longer than or equal to the second which is longer than the fourth. In the *rubriventris* complex, the third may be shorter than or equal to the second which is usually equal to the fourth. The first three free rib segments are nearly as broad as long in the *floridana* complex, whereas in the *rubriventris* complex these are twice as long as wide.

The posterior edge of the plastron is rarely notched in *picta* (less than one per cent of the population), but is usually notched in the other populations. The width of the anterior plastral segment compared to the posterior plastron varies from 0.90 in *picta* and *texana*, 0.94 in *concinna*, 0.96 in *scripta*, 0.98 in *nelsoni*, to 1.01 in *floridana*. The plastron in *floridana* has a noticeable outward bulge (convex) at the abdominal-pectoral scute seam in over 90 per cent of the specimens; other populations lack this bulge.

The posterior articular process of the sixth cervical vertebra (measured from the body of the vertebra caudad) is roughly half the length of its centrum in *nelsoni*, and one-third the length in *concinna* and *floridana*. That process in the seventh cervical vertebra is almost equal to the centrum length in *nelsoni*, but only two-thirds the centrum length in *concinna* and *floridana*. The angle formed by the junction of the acromium and scapula in *nelsoni* ranges between 100 and 105 degrees (mean, 103); *floridana*, 93-100 (mean, 95); *concinna*, 88-100 (93); *scripta*, 90-95 (93); and *picta* 80-97 (88). The angle formed by the coracoid and acromium (ranges and means in degrees): *concinna* and *scripta*, 51-60 (56); *floridana*, 42-53 (49); *nelsoni*, 40-46 (43); and *picta*, 40-50 (45). The epicondylar head of the humerus curls over the shaft in *concinna*, *floridana*, and *nelsoni* but not in *picta* or *scripta*. Other subtle differences in leg bones were found to be unreliable indicators to separate populations.

Although the color of head stripes and markings are useful at the species and subspecies level to differentiate populations (see Table 5), I could find little color distinction at the generic level. However, the presence of

TABLE 5.—Comparison of the head markings in three species of *Pseudemys* (sample size in parentheses). Numbers are the percentages of total species sample showing character.

Marking	<i>Pseudemys concinna</i> (111)	<i>Pseudemys floridana</i> (77)	<i>Pseudemys nelsoni</i> (40)
Hairpin head markings, both sides	0	70.6	25.0
Hairpin head markings, one side	6.5	23.5	0
Continuous chin markings	10.7	70.6	50.0
Noncontinuous chin markings	88.3	29.4	50.0
Chin markings form medial circle	48.4	41.2	25.0
Short lateral line from orbit	58.1	11.8	25.0
No short lateral line from orbit	41.9	88.2	75.0
Midsagittal widest dorsal stripe	35.5	88.2	75.0
Dorsal lines all equal or nearly so	64.5	11.8	25.0
Presence of anterior arrow	0	5.9	62.5
Small postsagittal Y or V present	45.2	17.6	0
Stripes between orbits: 3	6.5	70.6	50.0
Stripes between orbits: 4	6.5	5.9	25.0
Stripes between orbits: 5 or more	87.1	23.5	25.0
Postlabial stripe split:			
once into supralabial and infralabial	6.9	27.7	12.5
with orbital from supralabial	93.1	72.2	87.5
Three or more stripes touching			
posterior edge of orbit	54.8	5.9	12.5
Only one or two touching orbit	45.2	94.1	87.5

melanism in older animals is related to genera. Only males of the *rubriventris* complex show melanism, whereas neither sex in the *floridana* complex are melanistic. Both sexes are melanistic in *scripta*, but only females are in *picta*. Rubescence transcends all taxonomic distinctions, occurring in every population albeit in varying degrees. The *rubriventris* complex epitomizes the red shell tint, but certain *concinna* populations are strongly colored as well. Some *floridana* specimens have varying degrees of rubescence, but none extensively. Individuals from *scripta* and *picta* populations may have the borders of the carapace tinted reddish, or, as in the case of some *picta* populations, extensive red coloration may infuse the entire shell.

Inframarginal spots are useful for species differentiation. Large circular spots on the inframarginals in *nelsoni* occur anterior to the bridge and solid round blotches posterior to the bridge. Every inframarginal is marked. The circles are closed with thick periphery but very small center spot, and the posterior spots are found only on the scute just anterior to the seam. In *concinna*, the markings are all thick parenthetical shaped dark opened circles on each scute, anterior and posterior to the bridge. The arcs formed by the markings are on each side of the seam, with the seam evenly dividing the blotch. Dark, irregular shaped blotches occur just to the posterior edge of the bridge in *floridana*, with about two-thirds of the total marking being on the scute anterior to the seam. Dual circles of doubled lines occur around

each seam in *texana*. The inframarginal markings in *scripta* vary from solid spots to thick circles. In *picta*, these markings are extensions of the dorsal pattern.

Plastral patterns vary by species also. Dark pigment on each side of the seams follow the outline of each scute in *concinna*; however, this pattern, although typical of much of the range of the species, may be restricted to the anterior plastron or lacking altogether (particularly in northern and western specimens). In almost every specimen (99%) there is some dark pigment on the inguinal scute, which is the most useful character to distinguish *concinna* from *floridana*. Although normally lacking any markings on the plastron, *floridana* may have some markings of limited extent, but rarely on the inguinal scute (2%). Populations of the *rubriventris* complex may have plastral markings similar to those of *concinna* but restricted to the anterior plastron in many populations. Usually the plastral pattern is obliterated with age in the *rubriventris* complex. In *texana*, the plastral pattern is extensive in young animals, matching that of eastern populations of *concinna*; however, western populations of *concinna* have a very reduced plastral pattern, limited to the proximity of the seams.

The plastral patterns vary greatly in *scripta* populations, ranging from a single black spot on each gular scute to extensive mottling that covers most of the plastron. The patterns are more pronounced and well defined in hatchlings, whereas they become faded and irregular in older adults. Each subspecies has its own variational form of plastral pattern, although several share basic patterns.

Similarly, each subspecies of *picta* has a unique plastral pattern; the easternmost population has no plastral markings (*p. picta*), the westernmost population (*p. belli*) has an extensive figuring that covers most of the plastron, the northern middle west population (*p. marginata*) has a dark blotch confined to, but covering the entire middle third of the plastron, and the southcentral population (*p. dorsalis*) is virtually immaculate with a narrow band of dark pigment along the midline of the plastron in some specimens. The sole exception I found was a population of *picta* in North Carolina that had several individuals with a plastral pattern similar to that of the westernmost population, although less extensive in coverage. These could be intergrades from captive releases of the *belli* population in the area mating with local *picta*.

Systematic Relationships

Turtles are evolutionarily a conservative group, for they have evolved with only minor morphological changes. Sympatric turtle populations tend to adapt similarly to their shared environment so that a lack of extreme morphological variation exists between species. Therefore, turtle species sharing the same habitat may show little distinctiveness even when genetic integrity is rigidly maintained, that is, no interbreeding. Emydine turtles

typically show only minor differences among many species in response to the same selection pressures. Certainly in turtles, a successful major morphotype is repetitively utilized in any given environmental circumstance.

Of concern is the level of differentiation necessary between populations to justify separate nomenclature. Individual variation has been sufficient to justify naming even entire families of fossil turtles (see Hay, 1907, 1908; Gaffney, 1972; and others).

Interpretation of characters is the most difficult part of classifying organisms. Often polytypic species are named when individuals assumed to be morphological intermediates occur (Carr, 1935, 1938, 1952; Crenshaw, 1955; Milstead, 1969), although it is equally likely that some populations are distinct species sharing common characteristics. When two species or populations overlap considerably in characters, workers unfamiliar with the full range of variation become confused in their identification. Even if hybridization does occur in isolated populations, specific distinctiveness is not compromised (Mayr, 1966).

Turtles have evolved with little divergence and much convergence of characters due to their unique morphological adaptation being at once limiting and adaptively advantageous. Differentiation has been restricted, but small changes have had large effects in terms of speciation. Even Darwin (1859) recognized that variations in two or more species may resemble characters of each other, and that evolution proceeds by "insensible steps" which greatly change the nature of an organism or its parts. He further suggested that divergence was not a necessary contingency of evolution, particularly when the "conditions of life" remain but slightly altered.

The relationships of emydine turtles were considered based on evidence from many sources such as those mentioned above, but primarily on skull morphology. *Chrysemys* (*sensu* McDowell, 1964) was characterized by a lack of distinctiveness. The general shell shape is similar. The skulls of these species were indistinguishable to McDowell (1964) and to Rose and Weaver (1967).

But even McDowell (1964) recognized *Chrysemys picta* as an exception to many of the characteristics that he used to define the genus. Adler (1968) found nine distinguishing features between *Pseudemys* and *Chrysemys*. Galbreath (1948) noted 12 differences between *C. picta* and *P. scripta*. Winkour and Legler (1974) found *C. picta* was the only chrysemyd with rostral pores. Zug (1966) recognized subtle differences between the penis of *C. picta* and that of other chrysemyds. Ward (1970) discovered physiological differences between *C. picta* and *P. scripta* involving development of accessory respiratory organs and hypoxia tolerance. *Chrysemys picta* survived 20 per cent longer than did *P. scripta* at low temperature (5°C) in hypoxic conditions and twice as long at higher temperatures.

In view of the differences cited above, three genera are here recognized within the chrysemyds. *Chrysemys* is monotypic, *C. picta*, *Pseudemys* is composed of two species groups, herein formally recognized as subgenera: *Pseudemys*, (composed of two species, *concinna* and *floridana*) and *Ptchemys* (composed of *alabamensis*, *nelsoni*, *rubriventris*, and *texana*). *Trachemys* includes all *scripta* group turtles (but consideration is limited in this paper to only those populations north of Mexico). All three genera were distinct by the Pliocene, likely much earlier (Jackson, 1976; Weaver and Robertson, 1967). The three genera are recognizeably distinct, and workers have found it awkward to include them in a single genus (Holman, 1977) or even as subgenera (McDowell, 1964).

For taxonomic recognition, jaw structure is certainly most useful (Mayr, 1969; Gray, 1870) and is the major criterion in distinguishing chrysemyds. Additional evidence is provided by cranial myology, shell characters, noncranial skeletal elements, and physiologic evidence.

SYSTEMATIC ACCOUNTS

Chrysemys

Chrysemys Gray, 1844, Catalogue of tortoises, crocodiles and amphibians in the collection of the British Museum, p. 27.

Type species.—*Testudo picta* Schneider.

Content.—One species *Chrysemys picta*, with four subspecies recognized: *Chrysemys picta picta*, *C. p. belli*, *C. p. marginata*, and *C. p. dorsalis*.

Definition.—Small emydines, carapace length 11 to 18 centimeters (maximum, 25); shell without keel, rugosity or posterior notching; anterior marginals may be notched, cervical scute often notched medially; anal notch lacking; shell flat, height about 35 per cent of length (33-38); third rib longer than either fourth or second; angle formed by juncture of coracoid and acromium 45 degrees (40-50); angle of acromium and scapula 88 degrees (80-97); skull with narrow postorbital arch, narrow jugomaxillary arch, moderate zygomatic arch; premaxilla small, with medial notch; maxilla tomial ridge moderate, with tomiodont anteriorly; narial width usually greater than interorbital distance; skull width 65 to 71 per cent of length; prefrontal as wide as long; skull low, height at posterior orbit same as height at occiput; otic capsule long; temporal fossa narrow, width 41-47 per cent of length; prootic visible only as sliver on temporal shelf; upper jaw narrow (anterior width 26-28% of skull length, posterior 53-57%); maxilla lacks serrations; upper alveolar shelf narrow (12-14% skull length), with low median ridge without cusps; palatine contributes 30 to 35 per cent of alveolar shelf; mandible short; lower jaw wide, 90 to 100 per cent of length; dentary lacks serrations; lower alveolar shelf with one low cusp; external fossa deep; angular extends anteriorly beyond coronoid, prearticular does not; coronoid height twice the posterior mandible length, 28 to 32 per cent of mandible length; coronoid twice as high as lower alveolar shelf width;

adductor mandibularis pars profundus very large; pars superficialis also large; adductor mandibularis posterius small; adductor mandibularis anterior lacking, as are adductor mandibularis medialis and intramandibularis; zygomaticomandibularis present; red color often found in head and neck markings; shell with abundant red or reddish brown pigments; plastron with or without dark pattern; carapace width 73 to 79 per cent of length; carapace height 33 to 39 of length; plastron length 91 to 97 of carapace length; cervical scute 9 to 11 carapace length; cervical scute width 5 to 7 of carapace width; clutch size 2 to 10, maximum 20.

Remarks.—Range and diagnosis of subspecies are well covered in Ernst (1971), and I have little to add.

Pseudemys

Pseudemys Gray, 1855, Catalogue of the shield reptiles in the collection of the British Museum, Part I. Testudinata. British Museum, London, p. 197.

Type species.—*Testudo concinna* LeConte.

Content.—Six species are recognized: *Pseudemys alabamensis*, *P. concinna*, *P. floridana*, *P. nelsoni*, *P. rubriventris*, and *P. texana*, arranged in two subgenera, *Pseudemys* and *Ptychemys*.

Definition.—Large emydine, carapace length 20 to 30 centimeters in males, 30 to 40 in females (maximum, 42); shell rugose, without keel, with or without posterior notching; nuchal without notch; anal notch present; shell with low or high vaulting, height 37 to 44 per cent of length; second rib longer than third or fourth; angle formed by coracoid and acromium 43 to 56 degrees; angle of acromium and scapula 93 to 103 degrees; Skull: wide postorbital arch, wide jugal arch, and wide zygomatic arch; premaxilla large, usually (but not always) notched; maxillary tomial ridge large, with or without tomiodont; narial width greater than interorbital distance; skull width 69 to 75 per cent of length; prefrontal length short or long; skull roof high, height at posterior orbit greater than that at occiput; otic capsule long; temporal fossa moderately wide, width 43 to 55 per cent of length, prootic large, clearly visible on temporal shelf; upper jaw wide (anterior width 28-34% of skull length; posterior 59-63%); maxilla lacks serrations; upper alveolar shelf broad, 18 to 23 per cent of skull length, with elaborate ridging and cusping; palatine contributes 30 to 35 per cent of alveolar shelf; mandible width subequal to length; dentary with or without serrations; lower alveolar shelf with strong ridge with 2 to 6 sharply defined cusps; external fossa usually shallow, occasionally deep; angular and prearticular may extend anteriorly beyond coronoid; coronoid height subequal to posterior mandible length, 26 to 35 per cent of mandible length; lower alveolar shelf width 60 to 100 per cent of coronoid height; adductor mandibularis externus pars profundus and pars superficialis of moderate size; adductor mandibularis posterius very large; adductor mandibularis anterior present or not; adductor mandibularis medialis small to moderate

sized; intramandibularis and zygomaticomandibularis present; red color rarely found in head and neck markings except in juveniles; red color in shell abundant in some species, absent in others; plastron with or without dark pattern; carapace width 67 to 79 per cent of length; carapace height 34 to 48 of length; plastron length 84 to 94 of carapace length; cervical scute length 5 to 9 of carapace length; cervical scute width 2 to 8 of carapace width; clutch size 10 to 20, maximum 35.

Range.—Southeastern U.S., piedmont to coastal plains, north to central Missouri west of the Mississippi River and to west Texas.

Subgenus *Pseudemys*

Type species.—*Testudo concinna* LeConte.

Content.—Two polytypic species are recognized: *Pseudemys* (*Pseudemys*) *concinna* and *P. floridana*.

Definition.—Largest turtles in genus *Pseudemys*, carapace length to 42 cm.; carapace with only shallow rugosity in some adults (rarely in juveniles); posterior marginals with slight notch; plastron with deep anal notch; third free rib always longer than fourth, shorter than second; free ribs nearly as wide as long; angle formed by acromium and scapula less than 100 degrees; length of the posterior articular process of the sixth cervical vertebra about one-third the length of its centrum; inframarginal spots usually on scutes both fore and aft of seam, even posterior to bridge; melanism absent; postorbital arch very broad, about 18 per cent of skull length; prefrontal very short, width 105 to 177 of length; mandible short, as wide or wider than length; tomiodonts absent, or only slightly developed; several well-defined cusps on upper and lower alveolar shelves; angular and prearticular bones extend forward beyond coronoid; coronoid height over 30 of mandible length (29-34%); lower alveolar shelf width 60 to 70 of coronoid height; height of dentary greater than width of lingual shelf; adductor mandibularis anterior absent; intramandibularis and zygomaticomandibularis present; pterygoideus pars ventralis larger than the pars dorsalis; adductor mandibularis posterior and adductor mandibularis medialis small; cervical scute length 5 to 7 per cent of carapace length.

Pseudemys concinna

Testudo concinna LeConte, 1830, Ann. Lyceum Nat. Hist., New York, 3:106. Type not designated; type locality inferred: "Inhabits in the rivers of Georgia and Carolina, where the beds are rocky." Restricted to the vicinity of Columbia, South Carolina, by Schmidt (1953).

Emys annulifera Gray, 1831, Synopsis reptilium, 1:32

Emys hieroglyphica Holbrook, 1836, North American herpetology . . . , J. Dodson, Philadelphia, 1:111

Emys mobiliensis Holbrook, 1838, North American herpetology . . . , J. Dodson, Philadelphia, 1:71.

Emys labyrinthica Dumeril, 1851, Cat. Method. Coll. Rept., p. 13.

Ptychemys hoyi Agassiz, 1857, Contributions to the natural history . . . , Little, Brown & Co., Boston, 1:55.

Pseudemys elonae Brimley, 1928, J. Elisha Mitchell Sci. Soc., 44:67.

Pseudemys vioscana Brimley, 1928, J. Elisha Mitchell Sci. Soc., 44:66.

Pseudemys floridana suwanniensis Carr, 1937, Occas. Papers Mus. Zool. Univ. Michigan, 348:1

Content.—Five subspecies are recognized, *Pseudemys c. concinna*, *P. c. hieroglyphica*, *P. c. suwanniensis*, and two new subspecies described beyond.

Diagnosis.—A large species of subgenus *Pseudemys* to 42 cm. in carapace length; anterior extension of the cervical scute less than that of adjacent marginals; epiplastron with only shallow curve in cross-section; marginals V, VI, VII cover 80 to 85 per cent of the bridge; anterior width of combined XII marginals 58 to 64 per cent that of the posterior; height of posterior marginals (XII) 67 to 87 of anterior width, 42 to 52 of posterior width; carapace height 34 to 40 of length; angle of coracoid and acromium 51 to 60 degrees; mandible length usually greater than its width (width 96-110% of length); mandible upward flaring at the symphysis; lateral edge of lower alveolar shelf sweeps smoothly up to coronoid, not squared off; posterior mandible short; jaws U-shaped; symphyseal ridge prominent, raised (shallow in *P. floridana*, blending into alveolar shelf, see Table 6 for additional comparisons); lateral ridge with numerous serrations; external border of lower alveolar shelf slopes laterally from ridge; external fossa deep; posterior upper alveolar shelf greatly expanded; carapacial pattern open circles, particularly in young; black pigment on inguinal scutes always present, with or without plastral markings; plastron usually with dark figure, particularly in juveniles; inframarginal markings usually two equal black crescents enclosing seam; hatchling carapace length 36 to 40 millimeters (mean, 37.7); length of egg, 38-43 (mean, 40.3); often with red color on plastron and extremities; lateral head stripe with three minor stripes on either side (or vestiges); shell pattern on pleural scutes often with posteriorly directed open circle ending at edge of scute, although it may occur on any of the pleural scutes, it is usually on the second or third.

Remarks.—The diagnosis distinguishes *P. concinna* from *P. floridana*. LeConte (1830) differentiated between *Pseudemys concinna* and *P. floridana* on the basis of four main characters: 1) carapace pattern "varied, of differently formed lines" of yellow, "somewhat reticulate," with intervening spaces filled with short yellow lines in *P. concinna* as opposed to irregular lines of yellow, more or less radiating in *P. floridana*; 2) bridge with black longitudinal line; 3) upper jaw slightly serrated; 4) head markings with short thin line from the orbit between the postlabial and lateral, and the lateral and temporal stripes, opposed to no small lines between the postlabial, lateral or temporal stripes. Holbrook (1836-1838) paraphrased LeConte's descriptions (nearly verbatim), adding that the upper jaw was not serrated in *Pseudemys floridana*. Neither author mentioned a plastral pattern for either species. Holbrook (1836) described *P. hierogly-*

TABLE 6.—*Comparison of the mandibles of Pseudemys concinna and Pseudemys floridana.*

<i>Pseudemys concinna</i>	<i>Pseudemys floridana</i>
1. Symphysis pointed with flaring tip	Symphysis blunt, no tip
2. External border of alveolar shelf curves smoothly up to coronoid	External border squared off posteriorly
3. Posterior mandible length short	Posterior mandible long
4. Mandible appears U-shaped in horizontal section	Mandible V-shaped
5. Symphyseal ridge prominent, raised, steep	Symphyseal ridge shallow posteriorly, blends with alveolar shelf
6. External border of alveolar shelf slopes laterally from lateral ridge	External border of alveolar shelf straight from ridge
7. Lateral ridge with numerous denticulations	Lateral ridge smooth
8. Median ridge higher at symphysis	Median ridge lower at symphysis

phica in terms similar to those he used for *P. concinna*, neither species with plastral patterns but both with bridge markings, and *P. mobiliensis* (1838) with a dark plastral figure. Neither author associated bridge markings or plastral patterns with *P. floridana*.

Pseudemys concinna concinna

Range.—Piedmont and coastal plain of the eastern and southern states, from Virginia into Florida.

Diagnosis.—Pleural scute pattern of curved, black bordered, yellow lines, contained within the scute and may or may not be part of any continuous reticulate pattern; pleural I and II may have posteriorly facing, open figure of a half-formed, irregular rectangle perched on a short leg; in some northern populations, the pleural I may only have a slightly curved yellow line; midmarginal yellow stripe broad; plastron usually without extensive dark pattern, any dark markings limited to central seams; lower alveolar shelf width 16 to 20 per cent of skull length, 84 to 96 of coronoid height; skull width 67 to 73 of skull length; temporal fossa length 58 to 64 of total skull length; postorbital arch width 16 to 18 of skull length; zygomatic arch width 22 to 26 of skull length; anterior upper jaw width 47 to 51 of the posterior jaw width; carapace height 43 to 47 of width; intergular seam length 16 to 18 of plastron length; interfemoral seam 12 to 18 of plastron length; cervical scute length 7 to 9 of carapace length; postlabial, lateral and temporal head stripes nearly same width, lines between reduced to short mark from posterior orbit.

Remarks.—A differential diagnosis follows the description of *Pseudemys concinna metteri*.

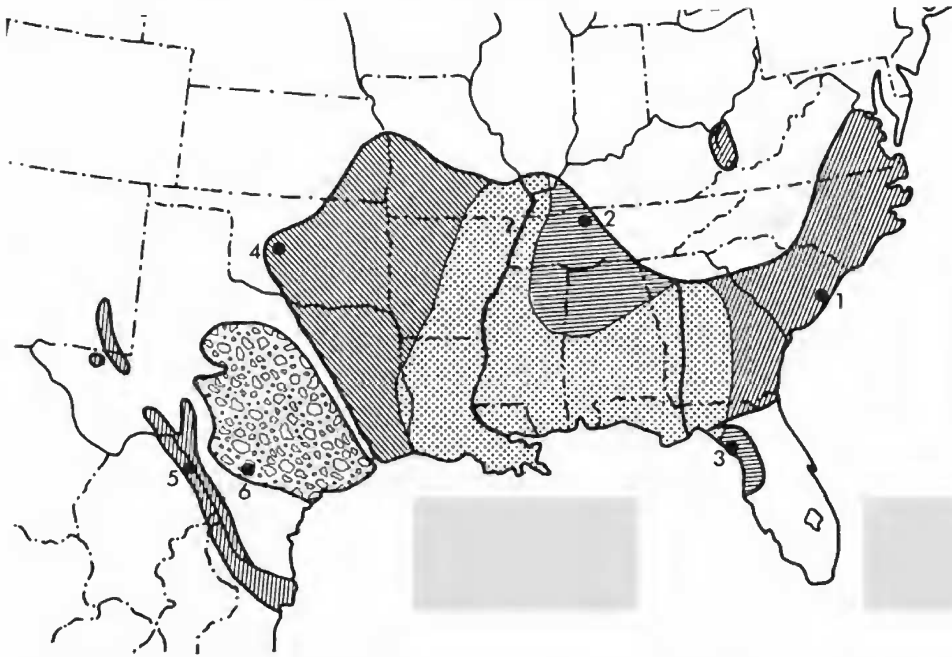


FIG. 5.—Range of *Pseudemys texana* and of the subspecies of *Pseudemys concinna*. Solid lines enclose the known ranges of each population. Circles indicate the type locality of each. The numbers indicate populations: 1) *Pseudemys concinna concinna*, 2) *Pseudemys concinna hieroglyphica*, 3) *Pseudemys concinna suwanniensis*, 4) *Pseudemys concinna metteri*, 5) *Pseudemys concinna gorzugi*, 6) *Pseudemys texana*. The dotted line encloses the area of known intergradation between subspecies of *Pseudemys concinna*.

Pseudemys concinna gorzugi, new subspecies

Holotype. Female, shell, skull, and skeleton, 39986, University of Kansas Museum of Natural History, from 3½ mi. W Jimenez, Río San Diego, Coahuila, México, 850 feet altitude, Peter S. Chraphrwy, 19 June 1952.

Paratypes.—KU 39985, 2 mi. W Jimenez, Río Diego, Coahuila, México; KU 15929 male, 20 mi. SW Carlsbad, Blue Springs, Eddy County, New Mexico; UU 4097 female, Black River, 7 mi. W Malaga, Eddy County, New Mexico, R. F. Bolland, 26 June 1963; UU 4110 male, same data as UU 4097; UU 4098 female, Río San Rodrigo, El Moral, Coahuila, México, J. M. Legler, 4-5 July 1963; UU 4107 male, same data as UU 4098; UU 4106 male, Evans's Creek, 15½ mi. NW Del Rio, Val Verde County, Texas, J. M. Legler, 1-2 July 1963; TTU 7347, hatchlings, 13 mi. SE Del Rio, Val Verde County, Texas, V. Procter, 7 April 1966; USNM 76, juvenile, near Cadereita, Nuevo Leon, Mexico, D. N. Couch; USNM 80, juvenile, Pecos River, Guadalupe Mountains, Texas, T. J. Pope.

Range.—Pecos River drainage of New Mexico and Texas; the lower Devil's River drainage, Rio Grande drainage from north of Del Rio, Val Verde County, to Brownsville, Cameron County, Texas; into México along

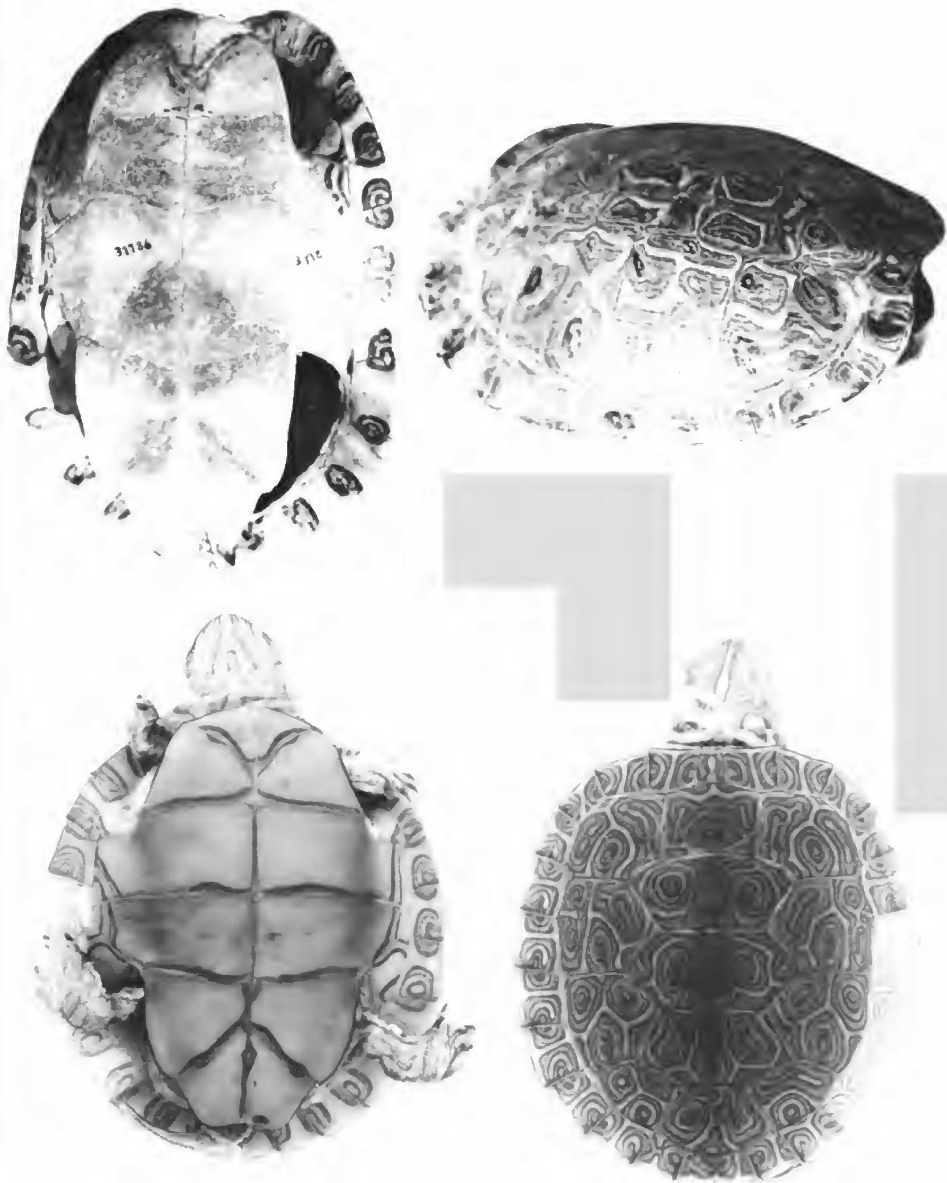


FIG. 6.—*Pseudemys concinna gorzugi*. Above, holotype (KU 39986); below, paratype (USNM 80).

the Rio Grande; restricted to the major river or within a few miles along tributaries.

Diagnosis.—A subspecies of *Pseudemys concinna* differing from other subspecies by: 1) pleural II pattern of five distinct whorls of concentric black and yellow ocelli enclosed in a thick, yellow framework—*P. c. hierogly-*

phica, *P. c. concinna*, and *P. c. suwanniensis* have thin, vermiculate patterns sometimes enclosing four ocellate figures; 2) lateral head stripe separated from orbit by small oval yellow spot; 3) inguinal scute very large, anteriorly nearly approaching the pectoral-abdominal seam; 4) skull with lower alveolar shelf width 19 to 20 per cent of skull length, 88 to 98 of coronoid height, skull width 75 to 83 of length, nares width 17 to 19 of skull length, coronoid height 26 to 30 of mandible length, upper alveolar shelf width 23 to 25 of skull length; mandible length 69 to 77 of skull length, orbit length 30 to 34 of skull length, temporal fossa length 81 to 85 of total skull length; 5) shell with interhumeral seam length 65 to 85 per cent of the interfemoral seam length; interpectoral seam 19 to 22 of plastron length; 6) plastron with thin, dark brown or black lines with irregular sides following the interscute seams on each scute but about twice the width of the line from the seam, never forming a complex figure or circular whorls.

Description of holotype.—Carapace oval, narrowing anteriorly; first marginals on both sides bow dorsally; widest point of shell at level of mid-scute pleural IV; rugose, but not deeply etched; margin strongly notched posteriorly at intermarginal seams 8/9, 9/10, 10/11, 11/12, 12/12; shallow notch at peripheral bone sutures 7/8, 8/9, 9/10, 10/11, 11/12; marginals rise dorsally beginning at marginal VIII posteriorly descending at marginal XI, dipping ventrally at seam between marginals XI and XII, rising dorsally to the seam between marginals XII; vertebral V with slight keel; slight bulge at level of pleural II.

Ground color of carapace greenish-brown with dark brown or black and yellow marking; markings consist of concentric black and yellow whorls separated by relatively broad yellow, curvilinear lines dividing each pleural scute II into four sections—the uppermost section elongate, longitudinally spanning the entire scute, the center two sections more rounded, the lower section partially divided and with two complete whorls; other pleural scutes with three sections of whorls; vertebral I urn-shaped with central whorl in posterior half; vertebral II and III with dual posterior whorls; vertebral IV with two anterior, one central, one posterior and two lateral whorls; marginals with black and yellow concentric ovals split by the inter-scute seam and separated by broad yellow, vertical bar.

Plastron narrow; anal notched; notched at anal-femoral seam; xiphiplastron flat; epiplastron rises anteriorly; intergular seam 15 per cent of plastron length, interhumeral 7, interpectoral 19, interabdominal 31, interfemoral 9, and interanal 22; anterior plastral lobe width 90 of posterior lobe width.

Ground color of plastron yellow; dark brown, thin line follows gular-humeral seam on both scutes, and part way along the humeral-pectoral seam; dual black lines run across the bridge from the anterior edge of the axillary scute to the posterior edge of the inguinal scute; inframarginal spots surround the interscute seams all around the shell.

Measurements of holotype.—Carapace length, 235 millimeters carapace width, 176; carapace height, 87; plastron length, 210; anterior plastral lobe

width, 88; posterior plastral lobe width, 97; skull length, 40; total skull length, 48.5; skull width, 30.

Variation.—Populations in Mexico, New Mexico and Texas (upper Rio Grande) have characteristic markings that have clinal variation. An hiatus of nearly 100 miles separates the New Mexico and Rio Grande populations due to the pollution of the intervening waterways by natural gas and oil field runoff.

The temporal head stripe is narrow in Texas specimens but is wide in others. The head markings of the subspecies are very different from other subspecies of *Pseudemys concinna*. There is a postorbital spot, yellow in color and oval in shape, that is as wide as the postlabial stripe. The temporal stripe curves dorsally over the postorbital spot and expands anteriorly, abruptly halting at the level of the postlabial split at the corner of the mouth. In some specimens, the temporal continues forward to the upper orbit as a thin line, but in most it terminates prior to the orbit. A smaller postorbital spot occurs just ventral to the larger, and terminates just anterior to an oblong spot situated in the tympanum. This latter spot is split from the lateral stripe and ends anteriorly at the level of the postlabial split. The postlabial splits at the corner of the mouth into the infralabial and a short supralabial, which terminates immediately after sending the orbital line dorsally to the ventral edge of the orbit. The lateral stripe is about half as wide as the postlabial and terminates anteriorly just prior to the tympanic spot. Between the lateral and the postlabial, a much thinner, yellow line parallels the course of the latter to the posterior edge of the orbit just dorsally to the end of the orbital. This thin line may terminate prior to reaching the orbit. At least one other line parallels the course of the temporal stripe but just ventral to it. Usually other thin lines and small spots are present between the major stripes.

The ventral symphyseal stripe is broad and runs into the ventral stripes at the point of the confluence of the ventrals. The ventrals join at the level of the posterior edge of the mandibular symphysis. The ventrals may continue, uninterrupted, posteriorly along the throat, expanding slightly, then narrowing, or may be broken on one side or the other. In some specimens, particularly those from New Mexico, the ventrals may converge again more posteriorly to form a circle with the symphyseal at one end and the two ventrals continuing posteriorly at the other end. The gular stripes are prominent and parallel the ventrals for most of their lengths. A medial stripe runs the length of the ventrals but midway between them. The medial is cut off when the ventrals form the circular figure, persisting only within the circle. The midsagittal is present on the dorsal head surface and is surrounded by two thin lines that parallel it. These two lines may converge posteriorly behind the midsagittal to form a single line, or may end prior to that point. The dorsal stripes are thin, and may join just posterior to the midsagittal and split around the latter to run to the posterior edge of the orbit or just above the orbit to the nose. When the dorsals join, an "X"

figure is formed. Both dorsals and the intermediate lines may be present simultaneously. A small postsagittal spot or "Y" may be present in some specimens.

New Mexico specimens have longitudinally directed whorls in the upper vertebral V, whereas these are circular in others. Texas specimens may lack the secondary lines between the orbits. Specimens from New Mexico have a yellow bar on the dorsal aspect of marginal X that is missing in other populations and that cuts the continuity of the circle across the seam between pleural IV and marginal X; whereas in other populations the circle is entire and no bar is found. Texas specimens tend to be darker than others. However, the New Mexico specimens have a dominating black blotch over the ventral portions of the intermarginal scute seams that is lacking in others.

Remarks.—This subspecies has been overlooked as being part of *Pseudemys texana*, to which it is superficially similar. However, the jaw structure immediately separates the two species. In addition, the carapacial markings on *P. texana* are thinner and organized differently. The whorls on the pleural II in *P. texana* are comparatively larger with thinner yellow framing and are oriented in a curving manner, sweeping dorsally and posteriorly when compared with *P. concinna*. The plastral patterns are quite distinct—*P. texana* has a more elaborate figuring on the plastron, with black lines extending well away from the seams, whereas in *P. concinna gorzugi* the lines rarely stray far from the seams. The posterior plastral area may have a figure formed by dashed or dotted lines in *P. texana*. The postlabial usually has a dorsally directed bar extending from a spot just posterior to the corner of the mouth in *P. texana*. The temporal and lateral stripes are the same size in *P. texana*, nearly indistinguishable from the other stripes.

Although not a whole, preserved animal, the specimen chosen as the type best displays the carapacial characteristics of the subspecies. Most preserved specimens darken rapidly so that most colors are indiscernible and the shell pattern is obscured. Inasmuch as many of the major features that separate *Pseudemys concinna* from *Pseudemys texana* involve skull structure, it is important that the type specimens readily show these characters.

Interestingly, no specimens of *Pseudemys concinna* have been naturally occurring in the fertile Lower Rio Grande Valley of southern Texas. The species only occurs on the Mexico side of the river in that area. However, further upstream, specimens are found on both sides of the river. Nowhere does *P. concinna gorzugi* achieve the high local populational densities that *P. texana* usually shows. Nor has *P. c. gorzugi* been found in the Big Bend region west of the Pecos River Canyon.

Etymology.—The subspecies is named in honor of George Zug, a good friend.

Pseudemys concinna metteri, new subspecies

Holotype.—Female, 7173, U.S. National Museum, Old Fort Cobb, Caddo County, Oklahoma, E. Palmer, 1 June 1868.

Paratypes.—UTACV-R-5163 females, Beaver's Bend State Park, McCurtain County, Oklahoma, J. R. Glidewell, 5 April 1975; TCWC 18462-1846 3 male, Jacksonville, Cherokee County, Texas, D. G. Groves, 18 April 1962; TCWC 14579, hatchling, 5 mi. N Humble, Harris County, Texas C. K. Winkler, 4 May 1957; TCWC 57934 female, Toledo Bend Reservoir, Newton County, Texas, no collector noted, 1 July 1974.

Range.—Mississippi River drainage from southern Missouri south to the Gulf of Mexico, west into western Oklahoma and northeastern Texas, from Dallas to Houston.

Diagnosis.—Pleural I with curved, yellow line, not connected with any extensive reticulate pattern; pleural II with vertical curved, yellow bar posteriorly, and another vertical line anteriorly situated on the scute; no partitioning into sections with enclosed whorls as typical of other subspecies; various curved thin lines are oriented in a vertical manner around the main bars on each scute; pleural IV often with posteriorly opened, semicircular line positioned low on the scute; midmarginal lines broad; head stripes narrow and numerous, with three minor lines between the postlabial and lateral and lateral and temporal stripes; plastron with extensive dark pattern; Skull: lower alveolar shelf width 14 to 16 per cent of skull length, 70 to 90 of coronoid height; skull width 71 to 73 of length; temporal fossa length 60 to 64 of total skull length; postorbital arch width 15 to 19 of skull length; Shell: interfemoral seam length 13 to 17 of plastron length; interanal seam length 19 to 21 of plastron length; cervical scute length 5 to 7 of carapace length.

Description of holotype.—Shell oval, widest at pleural III and IV seam; rugose; marginals strongly notched at seams posteriorly and slightly notched at peripheral sutures posteriorly; vertebral I very tiny, vertebral II elongated to include area vacated by I; vertebral V widest vertebral scute.

Ground color of carapace brownish, with yellow and black markings; markings on pleural II consist of three elements—an anterior, vertical yellow bar with rectangular expanded portion dorsally, outlined by thin black line; a central vertical yellow bar, broader than others, slightly curved with posteriorly directed, narrow process along upper scute seam; posteriorly, a very thin, vertical yellow line curving ventrally, then turning dorsally to parallel itself, ending at the midpoint of the posterior seam; pleural I with broad yellow, vertical bar expanded slightly dorsally in a triangular shape with the apex anterior and a thin line radiating anteriorly from the apex, branching into dorsovertical and horizontal components; pleural IV with H-shaped yellow line separating dual curved yellow lines; vertebrales with two yellow markings expanded in center; marginals with yellow bar in center.



FIG. 7.—Holotype (USNM 7173) of *Pseudemys concinna metteri*.

Plastron broad; anal notched; notched at anal-femoral seam; intergular seam 13 per cent of plastron length, interhumeral 10, interpectoral 15, interabdominal 29, interfemoral 13, interanal 19; anterior plastral lobe 98 of posterior lobe width.

Ground color of plastron yellow, with faint dark markings along anterior lobe seams and across bridge from axillary onto inguinal scutes; inframarginal markings dual black concentric circles enclosing seams.

Head broad; tomial ridge slightly serrated, lateral ridge strongly serrated; tomiodonts almost indistinguishable; ground color dark with yellow stripes; postlabial, lateral and temporal stripes distinct with three lines between each; temporal touches posterior edge of orbit, then continues along the dorsal edge of the orbit to end at the anterior edge, extending posteriorly to end of supraoccipital crest and expanding slightly; lateral begins at the posterior edge of the orbit and ends at the tympanum; the dorsal stripes run in wavy lines to converge anterior to the midsagittal along the upper edge

of the nose; the midsagittal has a short break at the level of the supraoccipital/frontal suture, then continues onto neck; posterior to the break in the midsagittal, five narrow lines occur on each side including the dorsals.

The symphyseal stripe is long and narrow, joining the ventrals, which run posteriorly without increasing size; a medial stripe runs along the ventral neck to terminate at the level of the articular condyles; thin lines parallel the medial on both sides then join anterior to the articular condyle area, continuing anteriorly as a single line for a short distance; gular stripes parallel the ventrals midway to the postlabials on either side; the postlabials branch at the corner of the mouth, forming the infralabials and an orbital on each side that does not reach the rim of the orbit.

Measurements of the holotype.—Carapace length, 268 millimeters; carapace width, 197; plastron length, 247; anterior plastral lobe width, 122; posterior plastral lobe width, 123.

Variation.—Pleural scute pattern varies individually from thin, straight bar to broad curving bar, but always vertically transects scute. Plastron pattern may be extensive or restricted to certain scutes. The inframarginal circles may be thick walled or with concentric circles. Western representatives are likely to have extensive reddish or coral color on plastra, whereas more northern specimens tend to be uniformly yellow on plastron.

Remarks.—Long confused with *Pseudemys concinna hieroglyphica*, *P. c. metterii* intergrades extensively with the former along a wide area extending from Missouri to Louisiana along the Mississippi River. The area of intergradation extends across most of the states of Mississippi, Alabama and into Georgia, involving further intergradation with *Pseudemys concinna concinna* and *P. c. suwanniensis* in Alabama, Georgia, and panhandle Florida. Clearly Holbrook (1836-1838) described the population from eastern Tennessee and Kentucky and northern Alabama as *Emys hieroglyphica* and an intergrade population in southern Alabama and Florida as *Emys mobiliensis*. Stejneger (1938) noticed the difference between *P. c. hieroglyphica* and populations of *P. concinna* from Oklahoma but erroneously assigned the latter to *P. texana*.

Pseudemys hoyi, Agassiz was revived by Stejneger (1938) to supply a name for variant populations in the Midwest, which he found perplexing. Agassiz (1857) never really used the term to identify a particular entity, but remarked that he had distinguished as *P. hoyi* specimens with a blunt head that he later found to be an embryonic feature sometimes preserved in older specimens. In any case, I have been unable to find genuine *P. floridana* west of the Mississippi River, or, in fact, west of the Black Warrior River in Alabama, nor anywhere within the supposed range of *P. f. hoyi*. Specimens I examined purported to be *P. f. hoyi* were easily referable to *P. concinna*. The broad, triturating surfaces and elaborate cusping of *P. concinna* populations, which are not found in *P. floridana* populations, are easily

seen characters that separate the two species. The presence of a dark marking on the inguinal scute in *P. concinna* is another reliable character.

The Louisiana population, recently assumed to be intermediate between *P. concinna* and *P. floridana* (Fahey 1980), is composed of *P. c. metter*i and *P. c. hieroglyphica* × *metter*i intergrades. Apparently, the confusion arises from the lack of plastral patterns in some populations but which is a characteristic of *P. c. hieroglyphica* as described by Holbrook. I have examined a number of specimens from Louisiana and East Texas without finding *P. floridana* influence. In fact, Fahey's (1980) own descriptions are all of specimens that fit within the normal variation of *P. c. hieroglyphica*, *P. c. metter*i, or expected in intergrade populations between the two subspecies.

Fahey (1980) assumed that all the populations represented by his specimens were intermediate because of the inconsistencies in the suite of characters he used to define the two species. I disagree with his conclusion that the plastral pattern has little taxonomic value. His assumption that "individuals with low scores," based on an assigned numbering system indicating the number of plastral scutes with dark pigments, were *Pseudemys floridana* stock is based on a geographically limited sample. Fahey's characters were limited because they were, in fact, drawn from an intermediate population—between subspecies of *P. concinna*. Unfortunately, Fahey used characters derived from a literature scan, from authors who apparently relied on characteristics of local populations rather than those derived from the variation over the entire range of the taxon examined.

Etymology.—The subspecies is named in honor of Dean E. Metter, long-time zoologist and mentor.

Differential diagnosis.—1) Pattern on pleural II composed of curved vertical bars not forming reticulate pattern in *Pseudemys concinna metter*i; forming four to five whorls (usually five) in spaces formed by wide yellow lines forming a reticulate pattern in *P. c. gorzugi*; pattern of yellow lines forming three or four spaces with indistinct whorls, wavy lines or whorls forming complete circles in *P. c. hieroglyphica* and *P. c. suwanniensis*; single stalked figure forming posteriorly opened semicircle or just random curved lines, enclosing other curved lines, sometimes whorls in *P. c. concinna*. 2) Plastron usually without dark pattern in *P. c. hieroglyphica*, with or without figure but normally confined to anterior plastron except in juveniles of *P. c. concinna*; plastron with extensive dark figure in *P. c. metter*i and *P. c. suwanniensis*; plastron with dark, globular curved lines along seams in *P. c. gorzugi*. 3) Head pattern of major stripes (postlabial, lateral and temporal) with three full or partial thin lines between the major stripes in *P. c. metter*i, *P. c. hieroglyphica*; *P. c. concinna* with major stripes with or without minor thin lines between; *P. c. suwanniensis* with reduced temporal stripe and reduced minor stripes between major stripes; *P. c. gorzugi* with lateral stripe broken into oblong spots posterior to orbit. 4)

Skull: postorbital width 16 to 18 per cent of skull length in *P. c. concinna*, 17 to 21 in *P. c. suwanniensis*, 16 to 20 in *P. c. hieroglyphica*, 15 to 19 in *P. c. metterii*, 18 to 22 in *P. c. gorzugi*; width of lower alveolar shelf 16 to 20 of skull length in *P. c. concinna*, 12 to 14 in *P. c. suwanniensis*, 13 to 17 in *P. c. hieroglyphica*, 14 to 18 in *P. c. metterii*, 19 to 20 in *P. c. gorzugi*, 55 to 71 of the coronoid height in *P. c. suwanniensis*, 60 to 74 in *P. c. hieroglyphica*, 70 to 88 in *P. c. metterii*, 80 to 100 in *P. c. concinna*, 89 to 100 in *P. c. gorzugi*; skull width 67 to 73 of skull length in *P. c. concinna*, 69 to 75 in *P. c. suwanniensis*, 71 to 73 in *P. c. metterii*, 73 to 79 in *P. c. hieroglyphica*, 75 to 83 in *P. c. gorzugi*; temporal fossa length 59 to 65 of total skull length in all but *P. c. gorzugi* where it is 81 to 85; width of zygomatic arch is 21 to 24 of skull length in *P. c. concinna* and *P. c. hieroglyphica*, 23 to 27 in *P. c. suwanniensis*, *P. c. metterii* and *P. c. gorzugi*. 5) Shell: intergular seam length 16 to 18 per cent of plastron length in *P. c. concinna*, 15 to 17 in *P. c. metterii* and *P. c. suwanniensis*, 14 to 16 in *P. c. hieroglyphica* and *P. c. gorzugi*; interhumeral seam 7 to 9 of plastron length in *P. c. concinna*, 6 to 8 in *P. c. gorzugi*, and 8 to 10 in the others; interabdominal seam 22 to 28 of plastron length in *P. c. concinna*, 29 to 33 in *P. c. gorzugi*, 25 to 29 in others; interfemoral seam 7 to 11 of plastron length in *P. c. gorzugi*, 11 to 18 in others; cervical scute width 4 to 6 of carapace width in *P. c. concinna*, 2 to 4 in *P. c. metterii*, 3 to 5 in others; cervical scute length is 7 to 9 of carapace length in *P. c. concinna*, 5 to 7 in others; carapace height is 43 to 47 of width in *P. c. concinna*, 44 to 54 in *P. c. gorzugi*, and 47 to 57 in others; anterior plastral lobe width 85 to 95 of posterior lobe width in *P. c. concinna*, 86 to 94 in *P. c. gorzugi*, 94 to 100 in *P. c. metterii*, and 90 to 96 in the others.

Pseudemys concinna hieroglyphica

Emys hieroglyphica Holbrook, 1836, North American herpetology. . . . J. Dodson, Philadelphia, 1:47. Type not designated; type locality, Cumberland River [Nashville, Davidson Co.], Tennessee.

Emys mobiliensis Holbrook, 1838, North American herpetology . . . , J. L. Dodson, Philadelphia, 1:71.

Pseudemys hoyi, Agassiz, 1857, Contributions to the natural history . . . , Little, Brown & Co., Boston, 1:55.

Range.—Southern Illinois into central Mississippi, east through northern Alabama into Georgia.

Diagnosis.—Pleurals with curved lines forming reticulate pattern of yellow outlined in black, forming small compartments within which are yellow spots with a single yellow circle around it or line with yellow oval or curved lines; midmarginal bars narrow; head stripes very narrow posteriorly, expanding anteriorly, prominent postlabial and infralabial and temporal stripes, with wide lateral stripe from posterior orbit to corner of mouth, then missing posteriorly in most specimens; plastron often without any dark pattern, or when present confined to anterior plastron; postorbital

arch width 16 to 20 per cent of skull length; skull height at orbit 38 to 40 of skull length; anterior upper jaw width about 32 of skull length, 45 to 57 of posterior jaw width; lower alveolar shelf width 16 to 17 of skull length; mandible width 105 to 112 of mandible length; interanal seam length 19 to 21 of plastron length; differs from *P. c. metteri* by: skull width 73 to 79 of skull length in *P. c. hieroglyphica* to 71 to 73 in *P. c. metteri*; interorbital width 24 to 28 of skull length to 21 to 23; interorbital width 82 to 98 of orbit length to 70 to 80; pterygoid width 30 to 34 of skull width to 27 to 29; premaxilla height 62 to 78 of maxilla height to 74 to 92; differs from *P. c. concinna* by: nares width 20 to 24 of skull length to 19 to 21 in *P. c. concinna*; skull width 73 to 79 of skull length to 67 to 73; interorbital width 24 to 28 of skull length to 19 to 23; lower alveolar shelf width 13 to 17 of skull length to 16 to 20; interorbital width 82 to 98 of orbit length to 62 to 78; coronoid height 31 to 37 of mandible length to 28 to 32.

Remarks.—The subspecies of *Pseudemys concinna* intergrade over a broad area covering most of the states of Mississippi and Alabama and the Florida panhandle. *Pseudemys c. mobiliensis* (Holbrook) is placed into synonymy with *P. c. hieroglyphica* (Holbrook). The type specimen (ANSP 242) appears to be an intergrade between *P. c. hieroglyphica* and *P. c. concinna*. The specimen is certainly that described by Holbrook (1838), but the population it represents is unquestionably intermediate and therefore his description is inappropriate. The type specimen also has several characteristics it shares with *P. c. suwanniensis* but is apparently separated from the latter by several dozen miles. I have been unable to find a distinctive population within the entire zone of intergradation of subspecies of *P. concinna*.

On the other hand, *Pseudemys floridana hoyi* (see remarks after *P. c. metteri* account) is simply another nonentity. It appears to be a confusion of the characteristics of both *P. c. metteri* and *P. c. hieroglyphica* and populations intermediate between them. I place *Pseudemys floridana hoyi* into synonymy with *P. concinna hieroglyphica*, from which it is indistinguishable. Although I had wondered about the inconsistencies of *P. f. hoyi*, I am indebted to Dr. James Dobie for first suggesting to me that it may not exist.

Pseudemys concinna suwanniensis

Pseudemys floridana suwanniensis Carr, 1937, Occas Papers Mus. Zool., Univ. Michigan, 348:4. Holotype, UMMZ 81673, Manatee Springs, Levy Co., Florida, A. Carr, 12 March 1934.

Range.—West coast of peninsular Florida from Tampa Bay to the Apalachicola River, extending inland only to Ocala, Marion Co.

Diagnosis.—Pleural I without differentiated line; midmarginal stripes thin, often Y-shaped; head stripes narrow (wide in *P. c. concinna*) and often indistinct in older individuals; plastron usually with extensive dark figure,

more evident in juveniles, and not restricted to the central plastron, often forming posteriorly directed swirls; postorbital arch width 17 to 21 per cent of skull length; skull height at orbit 41 to 45 of skull length; 104 to 110 of height at occiput; otic capsule 46 to 50 of skull length; width of upper jaw at anterior orbit 50 to 66 of width at posterior orbit, and approximately 35 of the skull length; premaxilla height 66 to 80 of maxilla height, 9 to 11 of skull length; mandible 63 to 67 of skull length; coronoid height 30 to 34 of mandible length; supraoccipital crest 9 to 19 of total skull length; cusping more elaborate than in other subspecies.

Remarks.—Carr erred in assuming that the darkened shell and skin of his type series typified the race. The darkening results from staining by the tannic acid in the Suwannee River from which Carr's sample came. Hatchlings and juveniles usually do not show the darkening, and rarely is the stain found in any other population. The stain also obliterates the red-tinged carapace and plastron that is found in other populations. The distinction between *Pseudemys c. suwanniensis* and *P. c. mobiliensis* is not real. I found the only features that separated the two were characteristics of the nominate subspecies influenced by intergradation. However, *P. c. suwanniensis* is more distinct from *P. c. concinna* and *P. c. hieroglyphica* than the latter two are from each other. All distinction breaks down along the northern Gulf Coast and any effort to assign any given population to a particular subspecies is virtually impossible.

Pseudemys floridana

Testudo floridana LeConte, 1830, Ann. Lyceum Nat. Hist., New York, 3:100. No type designated; type locality, St. John's River, Florida.

Pseudemys floridana, Baur, 1893, Proc. Amer. Philosophical Soc., 31:223.

Pseudemys floridana peninsularis Carr, 1938, Copeia, 1938:105.

Range.—Coastal plain of southern U.S. from North Carolina to the Mississippi River and throughout peninsular Florida.

Content.—Two subspecies recognized: *Pseudemys floridana floridana* and *P. f. peninsularis*.

Diagnosis.—A large species of the subgenus *Pseudemys*; anterior extent of cervical scute even with that of the marginals on either side; epiplastron with deep curve in cross-section; marginals V, VI, VII cover 82 to 90 per cent of bridge; anterior width of the combined XII marginals 69 ± 4 per cent of the posterior width; height of posterior marginals 57 to 75 of anterior width, 40 to 50 of the posterior width; carapace height 41 to 45 of its length (slightly higher in females than in males); angle formed between the coracoid and acromium 42 to 51 degrees; mandible width subequal to length, 94 to 102 per cent; mandible blunt, with no upward flaring tip; lateral edge of lower alveolar shelf squared off, upper and lower outer border terminating on same plane; posterior mandible length greater than in *Pseudemys concinna*; symphyseal ridge low, blending with alveolar shelf; lateral ridge without serrations; external border of lower alveolar shelf falls

perpendicularly from lateral ridge; external fossa shallow; alveolar shelf of upper jaw expanded posteriorly; carapacial pattern usually straight vertical lines; inguinal scute lacks any black markings; plastron usually lacks dark pattern, if present confined to anterior plastron; inframarginals spots solid blotches anterior to bridge, posterior to bridge most of spot anterior to seam; red color usually not present on shell or extremities; hatchlings with light stripe on lateral edges of marginals joining to form well defined circle completely around carapace; hatchling carapace length 31-34 millimeters (mean, 32.8); egg length, 34-37 (mean, 35.7); completely lacks tomiodonts; cusping on alveolar shelf reduced, usually only slight cusping on lower shelf; carapace height is 55 to 65 per cent of width (46-54 in *P. concinna*); cervical scute width 6 to 8 of carapace width (3-5 in *P. concinna*); anterior plastral lobe 96 to 106 of posterior width (90-98 in *P. concinna*); outer margins of anal scutes (xiphiplastron) converge posteriorly to form an angle 69 to 73 degrees to each other (40-54 in *P. concinna*).

Comments.—Subspecies are well defined by distribution with only a narrow zone of intergradation. Population previously considered as *Pseudemys floridana hoyi* not valid, relegated to synonymy of *P. concinna*.

The overlap of variation in characters between *Pseudemys concinna* and *P. floridana* has led to confusion regarding the separation of the two species. The confusion exists only when attempts to distinguish the two species are made based solely on color patterns. When morphology of the skull and shell are considered, the distinctiveness of the two species is readily apparent. I have found that, in emydines, color patterns are nebulous indicators of relationships unless the total variation of any particular species or population is well known. Such early confusion regarding the "red belly" of the *rubriventris* group led to speculations concerning hybridization (Carr and Crenshaw, 1957; Crenshaw, 1965), when none seems to actually exist.

Pseudemys floridana floridana

Testudo floridana LeConte, 1830. Ann. Lyceum Nat Hist., New York, 3:100.

Range.—Coastal plain from North Carolina to Louisiana, intergrading in northern Florida with *P. f. peninsularis*.

Diagnosis.—Subspecies of *P. floridana* slightly smaller than *P. f. peninsularis*; major character separating the two is the presence of hairpin stripes on *P. f. peninsularis*, just posterior to the orbits, which normally do not appear in the nominate subspecies; minor skull differences include: wider upper jaw in *P. f. floridana* (62-66% of skull length compared to 58-62), wider skull (72-76% of skull length to 69-73), wider pterygoids in *Pseudemys floridana peninsularis* (30-36% skull width to 29-31), longer otic capsule in *P. f. floridana* (51-53% of skull length to 47-49), wider lower alveolar shelf in *P. f. floridana* (70-84% of dentary symphyseal width to 65-73); the height of the skull at the orbit is 101 to 103 per cent that at the occiput in *P. f.*

floridana, 102 to 114 in *P. f. peninsularis*; inframarginal spots occur both anterior to, and occasionally, posterior to the bridge in *P. f. floridana*, only anterior to bridge in *P. f. peninsularis*.

Remarks.—The hairpin head markings that Carr used to separate *P. f. peninsularis* involves the confluence of the dorsal and temporal stripes just posterior to the orbit. However, this curve is also apparent in *P. f. floridana* but involves other elements and occurs farther back on the neck. The difference in sizes in the two subspecies is apparent when the two are compared. *P. f. peninsularis* is somewhat darker in color than is *P. f. floridana* and tends toward earlier obliteration of thinner head stripes.

Pseudemys floridana peninsularis

Pseudemys floridana peninsularis Carr, 1938, Copeia 1938:105. Holotype, MCZ 43849 female, Crystal Springs, Pasco Co., Florida, L. Marchand, 20 February 1938.

Range.—Peninsular Florida, south of 30°N latitude.

Diagnosis.—See previous subspecies. Major morphological difference involves the width of the lower alveolar shelf which is narrower in *P. f. peninsularis* than in the nominate subspecies. Hairpin head markings are the only easily recognizable point of separation.

Remarks.—The zone intergradation between the two subspecies actually encloses the type location of the species as given by LeConte. The species type is lost, but it is assumed that the description was of an intergrade. Because of the confusion as to the distinctiveness of the species *Pseudemys concinna* and *P. floridana*, consideration should be given to the designation of neotypes for both species.

Subgenus *Ptychemys* Agassiz

Type species.—*Testudo rubriventris* LeConte, 1830:100, designated as *Ptychemys rugosa* by Agassiz, 1857.

Content.—Four species, one polytypic; *Pseudemys (Ptychemys) nelsoni*, *P. alabamensis*, *P. texana*, and *P. rubriventris* (subspecies *P. r. rubriventris* and *P. r. bangsi*).

Definition.—A moderate sized *Pseudemys* group with carapace lengths 20 to 34 centimeters (rare maximum of 40 in one species, *P. rubriventris*); carapace strongly rugose, occasionally so even in juveniles; posterior marginals without notch; plastron with slight anal notch or very deep; third free rib length subequal to second or fourth; lengths of free ribs nearly twice the widths; angle formed by acromium and scapula over 100 degrees; length of posterior articular process of sixth cervical vertebra half the length of its centrum; inframarginal spots normally restricted to scute anterior to seam when aft of bridge; melanism present in adult males (rarely in females); postorbital arch relatively narrow, 16 ± 1.7 per cent of skull length; prefrontal moderate, subequal width to length; mandible width equals length; premaxilla with deep notch; tomiodonts present, well developed;

dentary strongly cusped, usually highly serrated; angular and articular bones extend forward beyond coronoid; coronoid height less than 30 per cent of mandible length, about equal to width of lower alveolar shelf; dentary height subequal to lingual shelf width; adductor mandibularis externus pars medius absent; adductor mandibularis anterior present; intramandibularis and zygomaticomandibularis absent; pterygoideus pars ventralis smaller than pars dorsalis; adductor mandibularis posterior and adductor mandibularis medialis well developed; abundant red pigment in shell and extremities.

Pseudemys (Ptychemys) alabamensis

Pseudemys alabamensis Baur, 1893, Proc. Amer. Philosophical Soc., 31:224. Holotype, USNM 20966 male, Mobile Bay, Alabama, G. Kohn, 7-11 May 1885.

Ptychemys mobiliensis Agassiz (part), 1857, Contributions to the natural history . . . , Little, Brown & Co., Boston, 1:55

Content.—Monotypic species.

Range.—Restricted to the Mobile Bay area of Alabama.

Diagnosis.—Member of subgenus *Ptychemys*; carapace low, rugose; plastron usually red or reddish orange in color; posterior marginals slightly serrated; pleurals with wide vertical bar, often Y-shape, yellow or red in color; temporal stripes over nares form prefrontal arrow; postorbital width 14 to 15 per cent of skull length; width of posterior upper jaw 64 to 66 of skull length; width of skull 73 to 77 of length; lower alveolar shelf 62 to 68 of mandible length; upper alveolar shelf width 23 to 25 of skull length; premaxilla height 78 ± 12 of the height of maxilla; lower alveolar shelf width 93 ± 6 of dentary width at symphysis; temporal fossa width 122 ± 9 of the orbit length. Shell rugosity and elaborate cusping of alveolar shelves separate this species from sympatric populations of subgenus *Pseudemys*. Tomiodentation separates *P. alabamensis* from *P. floridana* and the presence of a vertical line on the pleural scutes separates it from *P. concinna*.

Remarks.—*Pseudemys alabamensis* is a relict population of a group that apparently occupied the area exposed by the Wisconsin glaciation along the Gulf and Atlantic coasts, but which was cutoff when the sea level returned to present heights. *Pseudemys nelsoni* was likely close to the main stock of the group to which *P. rubriventris* and *P. texana* also belonged. *Pseudemys alabamensis* and *P. rubriventris* are allopatric by several hundred miles but occupy the same niche. Carr and Crenshaw (1957) identified two adults from the mouth of the Apalachicola River and from Jackson County, Florida, as *P. alabamensis*, but Mount (1975) reexamined the specimens and identified them as *P. nelsoni* (but see remarks on *P. nelsoni*).

Pseudemys (Ptychemys) nelsoni

Pseudemys nelsoni Carr, 1938, Occas. Papers Boston Soc. Nat. Hist., 8:307. Holotype, MCZ 39888 female, Fellsmore, Indian River County, Florida, G. Nelson, 1936.

Content.—Monotypic species.

Range.—Restricted to peninsular Florida.

Diagnosis.—Member of subgenus *Ptychemys*, with highly vaulted carapace, carapace height 40 to 48 per cent of length (females more vaulted than males); plastron often red or orange, particularly in males; posterior marginals only slightly serrate if at all; pleurals with wide yellow or red vertical bar, often Y-shape; temporal stripes form prefrontal arrow; distinguished from *Pseudemys alabamensis*, *P. rubriventris* and *P. texana* by reduced number of head stripes in adults; postorbital arch width 17-19 per cent of skull length; posterior width of upper jaw 59 to 63 of skull length; skull width 69 to 77 of length; upper alveolar shelf width 20 to 24 of skull length; lower alveolar shelf 60 to 66 of mandible length; premaxilla height 89 ± 12 of the maxilla height; lower alveolar shelf width 83 ± 5 of the dentary width at symphysis; temporal fossa width 115 ± 18 of orbit length. Tomiodentition and elaborate cusping separate *P. nelsoni* from sympatric *P. concinna* and *P. floridana*. Straight pleural bar separates *P. nelsoni* from *P. concinna*. *Pseudemys nelsoni* is immediately distinguished from sympatric *P. concinna* and *P. floridana* by the short interfemoral seam, 9 to 10 per cent plastron length compared to 11 to 16; by the relatively long cervical scute, 8 of carapace length compared to 5 to 7; and the relative lengths of the upper cervical scute to the lower portion (ventral/dorsal length is 55-65% in *P. nelsoni*, 23-43 in *P. concinna*, 34-52 in *P. floridana*). *Pseudemys nelsoni* is further separated from sympatric *P. floridana* by relative widths of dorsal and ventral cervical scute portions (ventral/dorsal 107-143% in *P. nelsoni*, 74-96 in *P. floridana*).

Remarks.—Fossil evidence indicates that *Pseudemys nelsoni* was once more widely distributed than now, ranging at least into South Carolina (Dobie and Jackson, 1979) and perhaps along the entire Gulf Coast as well. Crenshaw (1955) proposed that *P. nelsoni* is subspecifically related to *Pseudemys alabamensis*, hybridizes introgressively with *P. floridana*, and hybridizes with *P. concinna*. Carr and Crenshaw (1957) identified four juveniles from the Chipola River, Jackson Co., Florida, as *P. nelsoni*, and elevated it back to species rank. Having extensively collected in the Chipola River, and surrounding area, I am convinced that neither *P. nelsoni* nor *P. alabamensis* occurs in the Chipola River, or the Apalachicola River for that matter. Several juvenile *P. concinna* were found that fit many of the criteria for *P. nelsoni* used by Carr and Crenshaw, who seem to place undue emphasis on red coloration. I also have collected in areas with large populations of *P. concinna*, *P. floridana*, and *P. nelsoni* occurring together (Marion and Levy Counties, Florida) and found no evidence to support Crenshaw's (1955) assumption that extensive hybridization occurs between these species. Crenshaw (1955, 1965) was apparently unaware that *P. concinna* has extensive areas of red color on the shell (as do some populations of *P. floridana*); possibly this feature led him (and other

authors) to assume all turtles with red bellies are *P. alabamensis*, *P. nelsoni*, or *P. rubriventris*, or hybrids with those species. Moreover, specimens of *P. nelsoni* can have the hairpin head stripes of *P.f. peninsularis*, particularly on one side or the other (but not both). This is more true of populations in extreme south Florida, yet there is no indication that hybridization has occurred. In older specimens, particularly females, the elaborate cusping on the lower alveolar shelf is worn down nearly smooth in some specimens of *Ptychemys*, but the characters involving the femoral and cervical scutes remain.

Pseudemys (Ptychemys) texana

Pseudemys texana Baur, 1893, Proc. Amer. Philosophical Soc., 31:223. Holotype: ANSP 246 female, San Antonio, Texas, Dr. Hermann.

Ptychemys mobiliensis Agassiz (part), 1857, Contributions to the natural history . . . , Little, Brown & Co., 1:55

Pseudemys floridana texana Carr (part), 1938, Copeia, 1938:108.

Content.—Monotypic species.

Range.—Central Texas south of the Staked Plains, from the area of Big Spring, Abilene, and San Angelo in west-central Texas throughout the Colorado (Concho, Llano, San Saba), Brazos, Guadalupe, and San Antonio River drainages, to San Antonio Bay and Freeport in east-central Texas.

Diagnosis.—Member of subgenus *Ptychemys*, with low rugose shell, height 35 to 40 per cent of length, posteriorly serrated; plastron with anal notch; plastron seldom entirely red, but with red-tinged edge; pleurals with many curvilinear thin lines culminating in whorls, with 5 to 6 distinct rings (whorls) on Pleural II; inframarginals with concentric circles around seams, four curved lines anterior to seam, two to three posterior to seam in fairly straight lines; head with many thin stripes, with a bar posterior to orbit (from lateral stripe), and usually a short, vertical bar continuous with the postlabial stripe from just posterior to the jaw articulation, which causes other stripes above it to bend dorsally around it then back ventrally and forward; postorbital width 16 to 19 per cent of skull length; posterior width of upper jaw 57 to 63 of skull length; skull width 69 to 74 of skull length; upper alveolar shelf 59 to 64 of mandible length; premaxilla height 88 ± 12 that of maxilla; lower alveolar shelf width 89 ± 9 of dentary symphyseal width; temporal fossa width 108 ± 8 of orbit length.

Remarks.—The population of turtles previously known as *Pseudemys texana* was composed of two species, *P. concinna* and *P. texana*. The *P. concinna* segment was composed of *P. c. metterii* in northern Texas, and *P. c. gorzugi* in southern and western Texas. Carapace pattern and head stripes have been used to place *P. texana* in *P. concinna*, but if the *Graptemys* species and *Trachemys n. gaigeae* patterns from the same area are noted, similarities between them may indicate parallel evolution of morphotypes under similar selective pressures. Selection might have favored the evolution in the Southwest of a shell design that is ill adaptive elsewhere.

The paratypes in the U.S. National Museum (USNM 76, 80, and 7173) are all *Pseudemys concinna* and not *P. texana*. USNM 7173 is *P. c. metterii*, and the other two are hatchling *P. c. gorzugi*.

Pseudemys texana is parapatric with *P. c. gorzugi* in southern Texas. I have been unable to find both together, or within 50 miles of each other. On the other hand, *P. c. metterii* extends into North and East Texas as far as Dallas and Houston (UTACV-R-2998, 2999, 5010, 5011; TCWC 13967, 14579, 55088) and might overlap the range of *P. texana*, which has been taken as close as Possum Kingdom Lake in north-central Texas (UTACV-R-5081), but I have not seen evidence that the two species are sympatric. Nor have I found any evidence that indicates that the two species hybridize.

Pseudemys (Ptychemys) rubriventris

Testudo rubriventris LeConte, 1830, Ann. Lyceum Nat. Hist., New York, 3:101. Type not designated by LeConte; type locality, "Inhabit in rivers from New-Jersey to Virginia, chiefly, I believe, in such as are rocky; in the Delaware, near Trenton, they are numerous." Restricted to the Delaware River, near Trenton (New Jersey) by Baur, 1893.

Pseudemys rubriventris, Baur, 1893, Proc. Amer. Philos. Soc., 224.

Content.—Two subspecies recognized: *Pseudemys rubriventris rubriventris* and *P. r. bangsi*.

Range.—Coastal plain from New York to southern Virginia, with disjunct populations in Massachusetts.

Diagnosis.—Member of subgenus *Ptychemys*, with low, rugose shell, posteriorly serrated; plastron with anal notch; shell with abundant red pigments; pleurals with single wide, vertical bar, often Y-shape; temporal stripes form prefrontal arrow; postorbital arch width 13 to 15 per cent of skull length; upper alveolar shelf width 20 to 24 of skull length; skull width 71 to 75 of length; lower alveolar shelf length 60 to 62 of mandible length; premaxilla height 89 ± 14 of maxilla height; lower alveolar shelf width 91 ± 12 of symphyseal width of mandible; temporal fossa width 119 ± 7 of orbit length. Distinguished from sympatric *Pseudemys concinna* and *P. floridana* by extensive shell rugosity, tomiodentition and elaborate cusping of alveolar shelf. Individuals with worn alveolar shelf separated by the width of the lower alveolar shelf relative to skull length.

Remarks.—The similarities of shell color and shape between this species and *Pseudemys alabamensis* and *P. nelsoni*, as well as other features, indicate that these were perhaps continuous at one time. Subspecies are adequately covered by Babcock (1937). Misidentification could have prompted Crenshaw (1965) to assert that this species hybridizes with *Pseudemys concinna* in North Carolina.

Trachemys

Trachemys Agassiz, 1857, Contribution to the natural history of the United States of America, first monograph, Vol. 1, part 2, North American Testudinidae, Little, Brown & Co., Boston, p. 434.

Type species.—*Trachemys scripta*, Schoepff 1792.

Contents.—Possibly 16 species, six of which are polytypic. Only two occurring north of Mexico; *Trachemys scripta* and *Tigaigene*.

Definition.—A large emydine, carapace length 12 to 35 centimeters, males somewhat smaller than females; shell rugose, with keeled vertebral in adults; posterior marginals notched; nuchal notch absent; anal notched; shell of moderate height (about 40% of length); second free rib segment longer than third or fourth; angle formed by the coracoid and acromium 50 to 60 degrees; angle of acromium and scapula 90 to 95 degrees; skull with wide postorbital arch; jugal and zygomatic arches of moderate size; premaxilla large, notched; maxillary tomial ridge large, usually without tomiodonts; nares rarely wider than interorbital distance; skull width 68 to 76 per cent of length; prefrontal width equals length; skull roof high, height at posterior orbit less than that at occiput; otic capsule of moderate length; temporal fossa moderately wide, width 46 to 52 of length; prootic large, clearly visible on temporal ridge; upper jaw of moderate width (anterior width 30 to 40% of skull length, posterior 54-60%); maxilla serrated; upper alveolar shelf moderately wide, 15 to 19 of skull length; with low ridge and without cusps; palatine contributes 40 to 45 of alveolar shelf; mandible width less than length; dentary without serrations; lower alveolar shelf with single, low cusp; external fossa very shallow; angular extends forward beyond coronoid, prearticular does not; coronoid height equals posterior mandible length, 29 to 33 of mandible length; lower alveolar shelf width 54 to 57 of coronoid height; adductor mandibularis externus pars profundus of moderate size, pars superficialis small; adductor mandibularis posterius small; adductor mandibularis antierius present; adductor mandibularis medialis large; intramandibularis present, zygomaticomandibularis absent; lateral head stripes usually much larger than others, often red, particularly in females; plastron usually with some dark markings; clutch size 4 to 20, maximum 24.

Comments: Subsequent papers will deal with the relationships of the species and subspecies of *Trachemys*. All but one population of the genus occurring north of Mexico belong to the species *Trachemys scripta*. The population in the Big Bend area of Texas is the exception.

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Address of author: J. P. WARREN, 436 S. Star Ave., Panama City, Florida 32401.